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A CONTRIBUTION TO THE EMBRYOLOGY OF THE FORE-LIMB SKELETON.

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INTRODUCTORY.

THE concise account of the development of the human skeleton recently published in the Keibel and Mall *Text-book of Human Embryology* forms the standpoint of present knowledge of and opinion on the subject. Regarded from this standpoint, certain observations of some importance resulting from a study of the development of the shoulder girdle and fore-limb skeleton in man, recently undertaken by the writer, seem worthy of publication as supplementing the account of the cardinal features in the growth of these cartilages and giving an account of the early phenomena of the ossification of the scapula. In considering the observations made on the development of the skeletal arch which overhangs and strengthens the shoulder-joint, its origin from one of a smaller perimeter will be the chief subject of discussion.

The embryonic material employed consists of human embryos and fœtuses of from 10 to 30 mm. in greatest length, reconstructions of the fore-quarter skeletons being made in two cases, one a 20-millimetre and the other a 30-millimetre specimen. The specimens cited in comparison are in the Museum of the Royal College of Surgeons. As it is on the reconstructions that the initial observations were made and round them that the whole work centres, a short description of them forms the first part of this paper.

Technical Note.—In making the drawings of the cartilaginous skeleton, care was taken to indicate exactly the margins of the fully differentiated cartilage as contrasted with the transitional perichondrial layers in all cases except that of the clavicle in which the easily followed enveloping layer was shown.

Descriptive.

Model of the Fore-quarter Skeleton of a 20 mm. Human Embryo (figs. 1 and 2).

This model includes:—Twelve vertebræ of which the upper two are cervical, nine complete and two incomplete ribs, one lateral half of the sternum, all the elements of the limb and girdle skeleton.

The vertebræ are represented by their bodies, and continuous with these are the neural arches of the right side; cartilaginous continuity around the

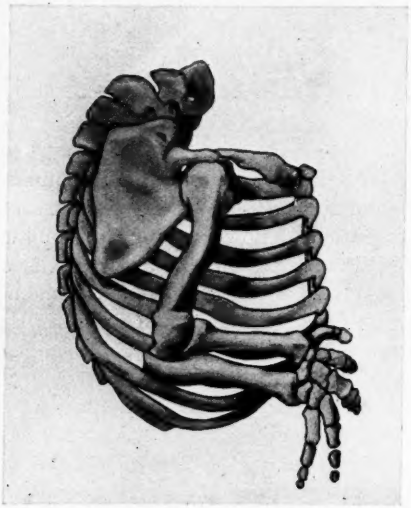

Fig. 1.—Wax-plate reconstruction from human embryo 20 mm. greatest length. Magnification in figure about × 8·5.

notochord exists between the bodies. They form a markedly arched series, the dorsal convexity being so great as to bring the two upper ones each rather ventral to the succeeding member of the series than on top of it; these two cervical vertebræ have procœlous bodies of approximately tetrahedral form, apex directed caudo-ventrally. The neural arches, imbricated above and in linear series below, show small lateral projections at their dorsal extremities representing demispines; the seventh cervical vertebra shows a separate chondral element, its costal process, which is in close articulation with the body.

The disproportionate length of the ribs and the approximately horizontal position each occupies give to the whole thoracic skeleton an

appearance of marked inspiration. In general the cross-section of each rib is circular, but in front there is dorso-ventral flattening, whilst behind the flattening is from above downwards; the anterior extremities of ribs I. to V. articulate with a delicate sternal bar of cartilage which merges above partly in the cellular nonchondral interclavicular mass; VI. and VII. meet and support each other caudal to the other extremity of this bar; all turn slightly dorsally, and I. to V. then acutely caudally in contact with the sternal bar. Like VI. and VII., VIII. IX. X. and XI. bend forward and so are disposed as in the adult.

The *clavicle* is represented in its inner four-fifths by a very stout bar prolonged as to its outer fifth in the form of a flattened plate by bevelling at the expense of its costal aspect. The curve of the lateral part of the adult bone is practically absent. The cellular constitution can be well

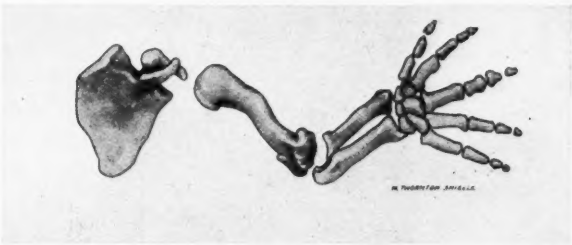

FIG. 2.—Wax-plate reconstruction from human embryo 20 mm. Schematic representation of scapula and limb skeleton. Magnification in figure × 7·14.

seen in fig. 6; it is made up of two ossific centres on the point of coalescence within a matrix of young cartilage cells, the whole being surrounded by a very dense cellular periosteum; this last is prolonged into (1) a cellular mass surrounding the tip of the acromion, (2) a similar mass at the opposite end, the inter-clavicle, and (3) a tract or band connecting behind the coracoid with the pre-scapula in which there is an appearance of early chondrification. The wedge of cartilage described by Professor Fawcett and assumed by him to be associated with the formation of the deltoid tubercle is well shown in fig. 6. In this figure the deltoid is not associated with it.

The *scapula* is as yet incompletely merged with the coracoid, as indicated by the width of the scapular notch and by a line of division across the glenoid cavity rather below its middle. The blade is irregularly diamond-shaped; its upper limit lies opposite the caudal extremity of the body of the sixth cervical vertebra, and its surfaces are parasagittal.

The *coracoid* is a bulbous mass of cartilage joined with the scapula by

a narrow neck and having a short cornuate process projecting upwards above the greater tuberosity of the humerus and a long one directed caudo-ventrally in the neighbourhood of the lesser tuberosity, considerably below the clavicle.

The *acromion* is a delicate bar showing an approximately right angle bend just above its root and a gentle curve beyond that to its tip, which projects slightly beyond the lateral extremity of the clavicle. Its root is immediately behind the edge of the scapular part of the glenoid cavity.

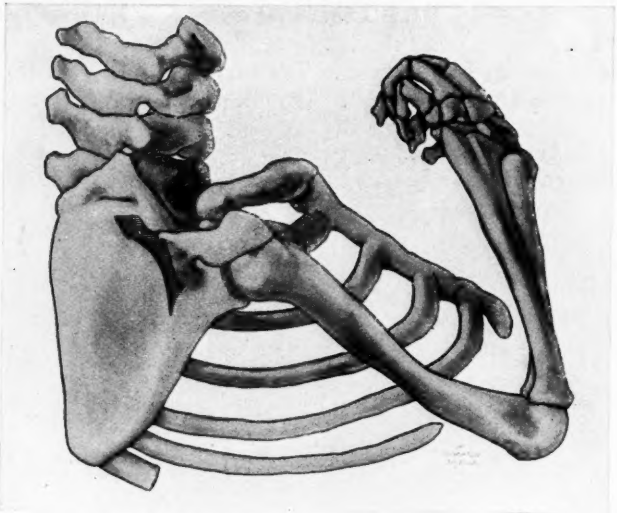

FIG. 3.—Wax-plate reconstruction from human embryo about 30 mm. greatest length. Magnification about × 8·5. Ossific plate shaded.

There is complete absence of the spine, but, on the other hand, there is present a distinct supraspinous element (which for reasons which will appear I will call the "prescapula"), separated by a slight interval near the middle of its length from the main part of the blade or "postscapula" and by a junctional zone dorsally to this. This prescapula is inclined at a slight angle to and occupies a more medial plane than the postscapula, as in fig. 5; a prominent ridge which lies on the superficial surface of the post-scapula, caudal to the interval between the two elements of the blade, indicates the future basis of support for the spine. By reason of this arrangement there exist two notches in this region, one which for my present purpose may be called coraco-prescapular, and becomes the future

incisura scapularis, and the other which I will call acromio-postscapular, a temporary feature later filled up by the growth of the spine. Between these two notches is the narrow area of origin of the supraspinatus muscle which occludes on one aspect the interval between the two parts of the blade.

The roots of the acromion and coracoid, and most markedly that of the prescapula, are invested by a thick layer of cells which surrounds the origin of supraspinatus and forms the scapular extremity of the previously

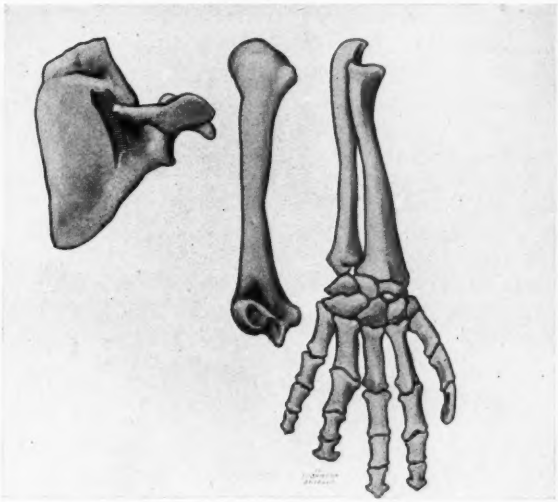

FIG. 4.—Wax-plate reconstruction from human embryo about 30 mm. Schematic representation of scapula and limb skeleton. Magnification about × 6.

mentioned band or cellular condensation which reaches behind the main mass of the coracoid to be continuous with the periosteum of the outer segment of the clavicle (fig. 6).

The *humerus* has a very remarkable shape. The shaft is bent outwards and forwards so as to form a salient angle opposite the deltoid insertion; its proximal half is arched outwards and its distal half backwards. Neither extremity in its relation to the axis of the shaft occupies a position corresponding to that of the adult bone; the proximal end is rotated somewhat outwards, and its articular surface is divided by a groove into two flattened condyles corresponding with the coracoid and scapular segments to which it is applied; the distal end occupies a plane such as

might result from a great exaggeration of that angle between the axis of the trochlea and the long axis of the shaft which is characteristic of the adult. By reason of this the inner lip of the trochlea forms the distal extremity of the humerus, and the capitulum lies on the lateral aspect at a higher level. A delicate outgrowth from the perichondrium of the shaft near its lower end ventro-lateral to the median nerve indicates the position of the entepicondylic spine (fig. 7).

What has been said of the distal articular surfaces of the humerus

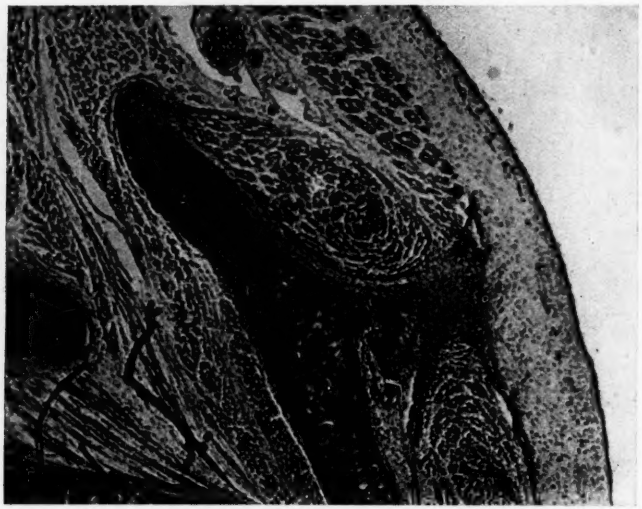

FIG. 5.—Coronal section, human embryo about 30 mm. Prescapula and postscapula, ossifying spine of scapula and trapezio-deltoid intersection.

conveys equally the relative position of the contiguous extremities of the *radius* and *ulna*. These two cartilages lie parallel, one above the other, but not quite in the same plane, owing to what may be described as a very slight degree of pronation. There is present between their distal ends an independent cartilaginous nodule embedded in a thickly crowded mass of cells. This may represent the intermedium.

Of the *carpal cartilages* those on the postaxial side are far in advance of those on the pre-axial side of the wrist; the same is true of the *metacarpals* and *phalanges*, the three digits of the ulnar side being almost equal in length and slightly longer than the index. End plates to the terminal phalanges are just recognisable by their dark staining and plexiform character.

Model of Fore-quarter Skeleton of 30 *mm. Human Fœtus* (figs. 3 and 4).

This reconstruction shows ten half-vertebræ, of which three are cervical, four complete, and three incomplete costal arches, the manubrium sterni, and representatives of three sternebræ and all the elements of the limb-girdle and free limb.

The position of the *vertebræ* has altered owing to the decrease of the

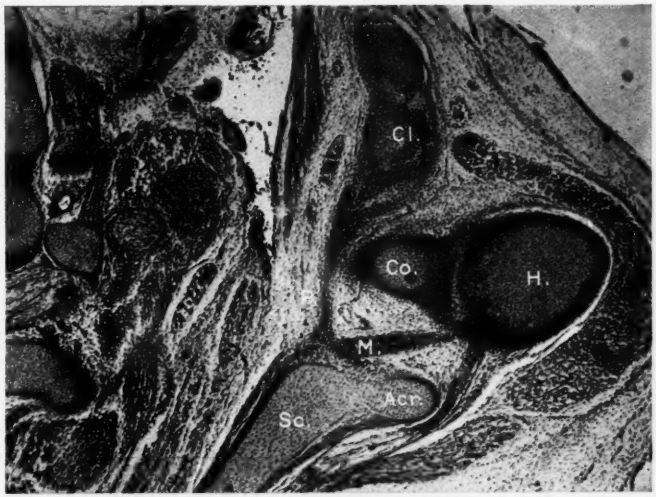

FIG. 6.—Horizontal section through shoulder of 20-mm. embryo.

Sc., scapula; Acr., acromion; H., humerus; Co., coracoid; Cl., clavicle; M., supraspinatus; and P., prescapulo-clavicular band shown attached dorsally where scapula is covered by thick cellular layer.

spinal curve, and the demispines on the extremities of the neural arches are now more marked. The *ribs* are now much more slender, except dorsally, where they are very massive and show commencing angulation.

The *manubrial cartilage* is pierced by a small hole, and there is a median cleft in the third sternebra.

The *clavicle* has developed rapidly, and has now almost the adult form with two curvatures; the outer extremity is, however, not so flattened as in the adult.

The *scapula* reaches headwards to the level of the caudal border of the seventh cervical vertebra; its diamond shape is still preserved, but the length of that border which runs from the coracoid to the upper angle has increased disproportionately; it follows that the "prescapular" bar is

greatly increased in size, the slit separating it from the postscapula has lengthened, and there is quite a marked groove indicating the boundary between the two elements and extending from the slit to the dorsal border, which it notches. The growth of the prescapula has greatly exceeded that of the postscapula in the 20–30 mm. period, and it now bears a greater proportion to the whole blade than does the resulting supraspinous part of the blade in the adult.

FIG. 7.—Horizontal section, human embryo 20 mm., to show:
H., humerus; R., radius in cartilaginous continuity; Med., median nerve with entepicondylic process of perichondrium on its lateral aspect (*).

The *coracoid* is little changed, being only rather smaller relatively.

The *glenoid surface* is now concave and undivided; it seems to have increased relatively in its lower blade part.

The *acromion* has grown considerably and become flattened and spatula-like, so that the acromial angle of the adult is now recognisable. The tip of the process projects considerably ventral to the outer end of the clavicle. The right-angle bend near the root described in the previous stage is now a sharp projecting elbow or spur of cartilage connecting with a tract of young, actively growing cells which passes backwards over the dorsum scapulæ, under cover of the small-celled fibrous intersection between trapezius and deltoid, nearly to the vertebral border. This tract represents

the developing spine, and in it, especially near the acromial elbow, ossification is well advanced (fig. 8). The ossifying region is shaded in the figures of the model, and it can be seen to extend into a projection at the scapular notch, over the edge of which it is continued on to the medial surface of the blade. The cells in which the ossification takes place are

FIG. 8.—Coronal section, human embryo 30 mm. Shows elbow of acromion and ossification of spine (*).

derived from the mass which in the 20-mm. stage clothed the roots of the postscapula, coracoid, and acromion.

The *humerus* is constricted in the region of spreading ossification, and is gently curved convex backwards. The two curvatures seen in the earlier stage are much less prominent in this later one owing to the great increase in length of the humerus, but both are easily identifiable still. The upper end is now only slightly out-turned as compared with that of the adult bone, and the lower end has assumed, in the inclination of its axis to that of the shaft, a position intermediate between that in

the earlier model and that representing the average of the two sexes in adult bones.

The *radius* and *ulna* likewise show constrictions in the ossifying zones. They are now very decidedly crossed. The ulnar styloid seems to be prolonged into the chondrifying discus articularis, and the same is true of the ulnar side of the lower extremity of the radius: between the two prolongations is a dense, unchondrified cell-mass. The contrast between this condition and that described for the 20-mm. stage is remarkable.

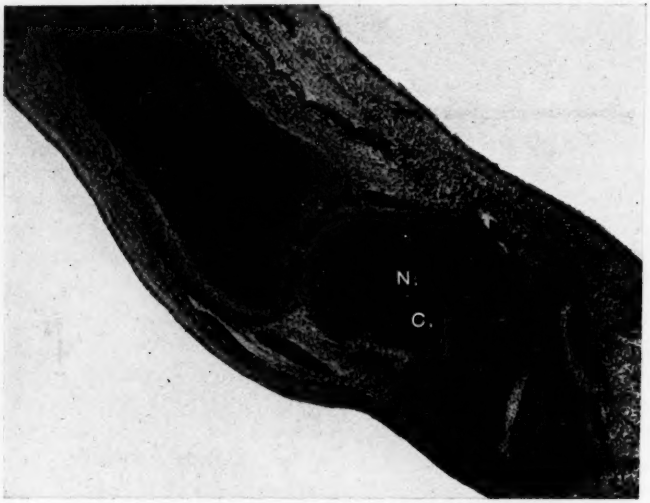

FIG. 9.—Coronal section, human embryo 30 mm.
C., centrale continuous through faintly staining zone with N., navicular.

The *carpal elements*, especially those of the distal row, are well forward in development, and there is visible, both on the palmar and dorsal aspects of the wrist, a distinct centrale; on that side it lies between navicular, lunar, and trapezoid, and on this between navicular, capitatum, and trapezoid; its surface isolation does not correspond with the conditions in the depth of the articulation, where it is continuous, through a faintly staining transitional zone, with the navicular (fig. 9). The navicular is in only narrow contact with the trapezium, which seems isolated at the radial end of the distal row and is slightly smaller than the trapezoid still.

The *metacarpals* and *phalanges* of the free digits are so disposed as to suggest that the hand is grasping a globe of small diameter. The end plates of the terminal phalanges are very broad.

Comparative.

In discussing the features of the models described, the opportunity of reference to other human embryos in the collection at the London Hospital will be made use of. These embryos comprise 8-mm., 10-mm., 15·5-mm., 24·5-mm., and 25-mm. stages, the measurements being in all cases those of greatest length.

The Vertebræ.—The position and the curious form of the cervical vertebræ in Model I. led me to seek in earlier stages for an explanation of the pointed caudal projection of their bodies. It is only in the cervical vertebræ that this condition is very marked, and at first it was thought to be purely a positional moulding. Naturally shape and position are related features in ontogeny, a fact which in this instance is confirmed by the

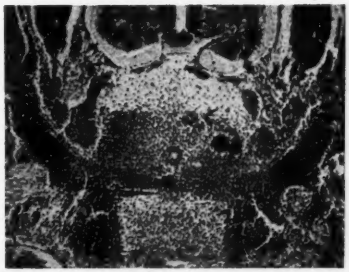

Fig. 10.—Human embryo 10 mm. Trans. section costo-hypochordal part of vertebral blastema shown stretching between the ventro-lateral myotome buds in front of chorda.

further observation that a much less and rapidly diminishing degree of the same moulding is visible in the upper thoracic bodies. Still, it seemed only reasonable to expect that the shape of the cervical and upper thoracic bodies in the adult, with their prominent ventro-caudal lips, would require for its production something more than a process of purely adaptive growth of the scleroblastema of what may be called the typical centrum. It remains to explain the two correlated features by means of some material organic addition to these vertebræ during their development; such an organic addition is provided for in the 10-mm. stage when there is present connecting the costal elements of all the upper vertebræ a hypochordal bar of condensed cellular tissue (fig. 10) into which the chondrification of the body can extend in a caudo-ventral direction. This extension will be facilitated by the positional relations of the upper vertebræ, which here form a more sharply curved arch than those lower in the series, where the hypochordal element is less easily identifiable. Lewis, in touching upon the hypochordal

element, limits it to the upper three cervical vertebræ and connects it, not with the costal, but with the neural arches. Bardeen notes its presence as low as the thoracic region.

The Ribs.—Apart from the excessive length of the ribs in relation to their average cross-section, the curve of the costal arches and the shape of the thoracic cavity resulting are noteworthy, since, in both models, the proportion between the depth and breadth of this is reversed as compared with the adult form; further, the cylindrical form of the earlier stage is seen to be transformed into a truncated cone in the later, the profile view of which shows it to be much blunter than after completion of its full growth and expansion. In Model I. the ventral ends of the ribs are free, with the exception of the first, which is fused with the sternal bar, whilst the second, third, fourth, and fifth turn caudally alongside it, being accommodated in fossæ on its lateral aspect; in Model II. these have fused with the side of the sternum. The cartilaginous sternal bar ends, in the 20-mm. stage, opposite the fifth rib, and the ventral extremities of the lower ribs turn headwards, the sixth and seventh ending in a condensed blastema continuous with the cartilaginous sternum. It would thus appear that the thoracic skeleton is furthest advanced in development at its inlet, and that the fusion between rib and sternal cartilages is a secondary process, like the fusion of the sternebral halves, as seen occurring in the third body sternebra of the 30-mm. stage. The use of the term "sternebra" in blastemal and cartilaginous stages is of course unjustifiable, but it has been employed for convenience sake to designate those parts of the continuous bar or bars which correspond to the bony segments of later stages.

The Clavicle.—The form of the clavicle in Model I. is very striking by reason of the absence of that curvature which characterises its outer segment in Model II. and in the adult. In the 10-mm. stage, which may be taken as the equivalent of that, *i.e.* 10·5 mm., described by Lewis, the blastematous clavicle extends inwards only one-third of the distance to the ventral end of the first rib, which it reaches in the 15·5-mm. stage. Arrived at this stage in its growth, the clavicle is therefore represented only by that part which, if form be any criterion, is the equivalent, in the adult, of its inner two-thirds at most; at this stage it seems to halt until a short time before that represented in Model I.; then begins a further and distinct stage in growth coincident with the onset of ossification, one in which the lateral third of the clavicle of the adult is evolved from the cellular mass at the distal end (fig. 11). In this way the clavicle achieves its full development, arriving at the condition seen in Model II. The striking difference in the two stages of the development of a bone whose two parts are just as strikingly different in the adult, separated as those

stages are by a considerable period of time, seems to warrant that any theory of the growth of the clavicle should take full cognisance of the causal facts that in the first stage the growth is axipetal, in the second, axifugal. It may be contended that the axifugal growth of the outer segment here emphasised is undeserving of emphasis, since it is equalled

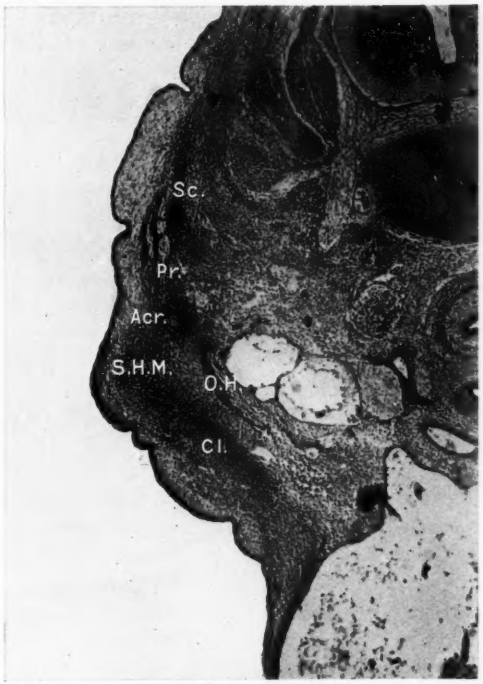

FIG. 11.—Horizontal section, human embryo 15·5 mm.
Cl., clavicle continuous laterally with suprahumeral cell mass (S.H.M.); Pr., prescapula; Sc., postscapula; Acr., acromion; O.H., omohyoid.

by contemporary axipetal growth of the inner segment; but it must be remembered, on the contrary, that the proportionate increase of the two growing ends differs widely and remains in favour of the outer, otherwise no such change in shape as occurs between that in Model I. and that in Model II. would take place.

The Scapula.—The most striking features of the growth of the scapula, as brought out by the two models, are the development of the supraspinous portion of the blade and the late appearance and mode of origin of the

spine. The partial separation of the growing cartilage which represents the supraspinous part of the blade, to which the name prescapula has been given, especially excites curiosity. This separation is first fully recognisable in the 15·5-mm. embryo (fig. 11), and reaches its greatest differentiation in that represented by Model II.; it is the more remarkable in that the slit seen in the two models between pre- and postscapula is occupied only by cells of the limiting membranes or perichondria of the two parts (fig. 5), and is not a passage for vessels or nerve filaments. For this reason it is to be considered a truly morphological separation, and not merely a casual fenestration, such as is a noticeable feature of the cartilages of certain amphibian and reptilian shoulder girdles. It is further especially to be remarked that the prescapular segment is fully continuous with the rest of the blade laterally, where it bounds the scapular notch, and that, at its other extremity, it is marked off from the blade in both models by a distinct groove and projects somewhat from the vertebral border, where it forms a part of this; in the former situation also it has a decided ventral projection clothed by a distinct cell-mass, among the surface layers of which the fibres of origin of supraspinatus are interspersed. A comparable condition is found in the scapula of the dolphin, *Delphinus delphis* (fig. 12 (III.)), a condition made the more noteworthy by the absence of anything resembling a true acromion process. In the toothed whale, on the other hand, an acromion process is seemingly present, but the prescapular equivalent is absent to all appearances (fig. 12 (I.)), whilst in *Mesoplodon Grayii* a condition is present which can be regarded as an intermediate stage between the two; in it, to adopt the accepted terminology, the acromium is bent backwards into a prescapular position, without, however, becoming continuous with the blade at its vertebral extremity (fig. 12 (II.)). Here, seemingly, are three stages in the formation of a prescapular element out of what has been previously considered an acromion process—an assumption which, in the absence of the clavicle and the scapular spine among Cetacea must, for the moment, remain a doubtful quantity. There is, then, in the development of the human scapula an element, the true morphological importance of which has hitherto been disregarded, and which I have called the prescapula, whilst in the scapula of the adult dolphin a similar element is separable which, in its turn, is to be compared with the so-called acromion of *Mesoplodon Grayii* and of the toothed whale.

Turning to the development of the spine of the scapula, we find that appearances indicate an origin for it in a cellular proliferation connecting with the elbow or spur of the developing acromion process (as distinct from the adult acromial angle); this undergoes a precocious ossification (fig. 8) as it spreads dorsally under the trapezius-deltoid intersection from the

region of the scapular notch. The nature of the cells is, from their appearance alone, not easy to discern, but such characteristics as they

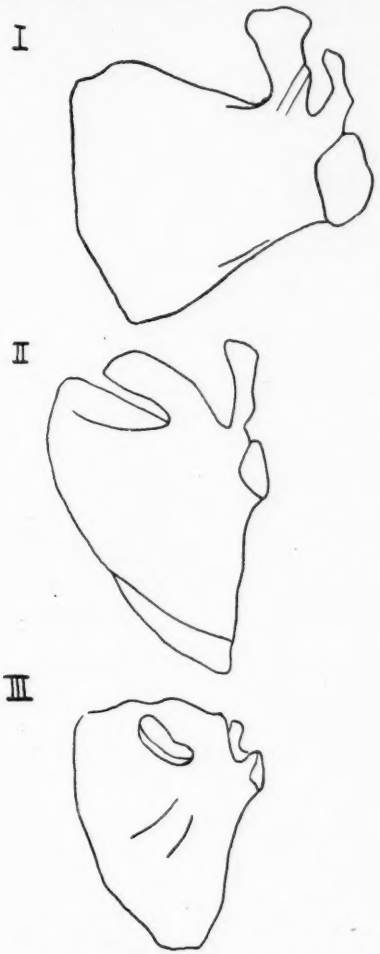

FIG. 12.—I., Scapula of *Physeter Macrocephalus*; II., Scapula of *Mesoplodon Grayii*; III., Scapula of *Delphinus delphis*.

possess, coupled with their secondary continuity with the fully differentiated cartilage of the acromial elbow, places them as derivatives of cartilage cells. Perhaps the most striking fact brought out by the second model

is the formation of a bony dorsal boundary to the scapular notch through the agency of cells which in the 30-mm. stage are continuous with those ossifying under the acromion, and which are only represented in the 20-mm. stage by the mass lying most thickly at the root of the prescapula. The position and relations of this cellular proliferation are very suggestive, especially in view of the ossific process which takes place in it so early after its assumption of rapid growth. Firstly, it overlies the junctional zone between coracoid and scapula; secondly, it lies at the dorsal extremity of a band of thickly crowded cells which passes medial to the coracoid (figs. 6 and 11) to divide into three well-marked strands merging with the periosteal layer of the outer segment of the clavicle; thirdly, this connexion is identifiable in the 15·5-mm. embryo as a dense strand forming the mesial boundary of a cell-mass which includes more laterally the prechondral representatives of acromion and clavicle, the middle of which is less condensed than its mesial and lateral margins. The mesial margin is well seen in fig. 11, and can be traced dorsally to the nucleus of chondrification representing the prescapular element and ventrally to the clavicle, whilst the middle third of it gives origin to the omohyoid, just lateral to the subclavian vein. The ossification of the scapula commencing at a junctional zone is remarkable as a parallel phenomenon to that described by Professor Fawcett in the ossification of the clavicle; closer examination may show even greater resemblance in the details of the process; whilst further, in view of the importance of junctional zones as centres of growth, brought out by the work of Professor Geddes on the Vertebrate Limb, an even more widely generalised significance may be attributable to this fact in the growth of the scapula. The cell strand connecting prescapula and clavicle is so far differentiated in fig. 6 that it represents the typical position of those ligamentous fibres which in many adults pass along the upper part of the conoid ligament into the transverse ligament; in this figure the omohyoid origin is not connected with these fibres, a fact which is referable to the dorsal migration of the origin towards the scapula.

The explanation of the observed facts bases itself mainly upon the presence of the large cell-mass in the upper shoulder region in the 15·5-mm. stage. This mass is continuous with the acromion laterally, with the prescapula dorsally, and with the outer extremity of the chondrifying clavicular bar ventrally. It is in this mass that the specialisation of the clavicle-acromion arch so closely related to the evolution of a freely movable shoulder-joint must occur, and, since this specialisation is especially important in man, the steps of its development may be expected to abound in matter for comparison with the vertebrate girdles down even to those

of the reptilia. Taking into consideration the variety of forms among the mammalia assumed by these portions of the skeleton, the cell-masses which are their precursors in ontogeny must be regarded as possessing a remarkable degree of lability, and, for this very reason, as being likely to preserve in the stages of their early development certain main features of their common and very early precursors in phylogeny. The earliest form of the human shoulder girdle, as figured by Lewis for a 10·5-mm. embryo, is a rectangular mass of crowded cells representing a scapula and situated high in the cervical region, to all appearance a plate-like headward prolongation of the axial condensation of the free limb. In it, again, according to Lewis's figure, there is a shallow furrow which may or may not be the first indication of the slit found in the cartilaginous scapula of later stages; if it be not, I am inclined strongly to the view that this rectangular mass of cells represents rather the prescapula of the cartilage stages than the postscapula, and from its caudo-lateral angle the postscapula may grow out; this view would be little more than speculation if it were not that the prescapula of a 15·5-mm. embryo shows a more advanced stage of differentiation than does the rest of the scapula. This is, however, a point on which the material at my disposal does not provide any further evidence of conclusive value, and which is of minor importance for the further development of the deductions made from the other facts observed in order to elucidate the connexion of prescapula and clavicle. This connexion has been fully described and figured, as has also the evolution of the so-called acromion in the Cetacea, through which it becomes converted in *Delphinus delphis* into a remarkable semblance of the human cartilaginous prescapula; and it only remains, in the first place, to emphasise that the connexion of the human prescapula with the clavicle is made at the mesial extremity of the lateral segment of the clavicle, and, in the second place, to postulate that the Cetacean so-called acromion connected with the clavicle of Cetacean progenitors, in order to reach the conclusion that the labile substance of the shoulder region can produce under evolution a mesial and a lateral arch; that one prescapulo-palæoclavicular — possibly identifiable in Cetacean ontogeny—this one acromio-neoclavicular in nature. In support of this conclusion and of the one postulate furthering it are a number of indisputable facts:—

1. That the ingrowth of the clavicle in stages from 10 mm. onwards occurs, not from the region of the tip of the acromion (*sensu stricto* as here applied), but from the ventral extremity of the strand of cells which forms the mesial limit of the suprahumeral arch mass, the outer periphery of which will later give rise to the outer segment of the clavicle ventrally and to the acromion dorsally. This is beautifully demonstrated in fig. 11,

15·5, which, it will be remembered, comes from a stage 15·5 mm., in which the clavicle has reached to the ventral extremity of the first rib.

2. That the variations in origin of the posterior belly of the omohyoid muscle almost never follow the lateral or acromio-clavicular, but nearly always the mesial or prescapulo-precoracoid arch.

3. That in the two-toed sloth, *Cholœpus Hoffmannii*, the prescapula and acromion are synostosed, and with the complete arch thus constituted from the periphery of the suprahumeral mass the clavicle articulates, which clavicle, to judge by its sole curvature, a ventral convexity, represents only the precoracoid portion of that bone (fig. 13). By reason of the primitive scale of general mammalian organisation found in the Edentata, and also by reason of the habits of the sloth, this fact supports both the conclusion I

FIG. 13.—Scapula. Clavicle of two-toed sloth, *Cholœpus Hoffmannii*, showing acromio-prescapular arch.

have come to and the postulate regarding the Cetacean clavicle necessary to its validity in the comparative sense.

To summarise, the shoulder arch in man shows in its development a fair epitome of the phylogenetic steps in its specialisation from a type which would be fairly represented by the shoulder girdle of the toothed whale, did this possess a clavicle, a type extant in both Ornithorhynchus and Echidna. With advancing specialisation the original arch becomes converted to other uses; the primitive acromion becomes the supraspinous plate, and a new acromion is evolved, whose earliest trace is possibly identifiable in Echidna and whose intermediate form is exemplified in the sloth, this new acromion having a wider sweep and necessitating an addition to the primitive clavicle. Meanwhile the intermediate portion of the original arch merges in, or specialises as the transverse and part of the conoid ligaments of man.

This theory of the development of two arches in the mammalian shoulder girdle deserves a reference to the conditions in lower vertebrates. In the reptiles the so-called clavicle often reaches far on to the dorsum of the

scapula, whilst as yet no acromion can be said to exist, indeed the dorsal portion of the clavicle occupies a position on the reptilian scapula which is only comparable with that of the scapular spine in man, or in other mammals in which a truly homologous spine is developed. Such an extension of the clavicle may reasonably be supposed, I think, to follow the line of our prescapulo-precoracoid arch, and thus leads on to the hypothesis that that cellular covering of the root of the prescapula (fig. 6) which ossifies to form a bony spicule, the definitive dorsal edge of the scapular notch, and which further extends to the root of the acromion and under the trapezius-deltoid intersection to form the spine of the scapula, ossifying as it goes, is the homologue of part of the original reptilian clavicle. This is only, however, a hypothesis, but it has so many favourable features that it seems worthy of the more exhaustive examination of embryonic and comparative material necessary for its proof and acceptance as a well-grounded theory.

The secondary coalescence of spine and acromion would well account for the proliferation which forms a spur on the acromial elbow in Model II., and a similar but more marked outgrowth in this junctional zone doubtless results in the formation of a metacromion as found in certain rodents, and markedly in the elephant. For particularly directing my attention to this structure, I am indebted to Professor Wright.

The *humerus* in the forms in which it appears in Models I. and II. is a very interesting object. Its curvatures are striking, and the torsion and angulation of its upper and lower extremities are brought out in a way which previously figured reconstructions have failed to indicate. This is to be attributed to the method I have adopted of drawing only the limits of the cartilage and avoiding the perichondrium, at stages in development when the differentiation of that tissue has reached or slightly overstepped its "optimum." The seeming contrast between the two forms is dispelled on close examination of the second model, and the change is attributable only to the enormously increased length of the shaft and its relatively decreased girth in the region of the primary ossification. Distortions of the shafts of long bones have been noted in embryo by Holl, Schomberg, and others, and attributed to disproportionately rapid growth in length; these are especially marked in hardened specimens and are therefore probably artificial. Of such artificiality I see no trace in the developing humerus, either in Lewis's figures or my own material, and I consider that both the described curvatures of the shaft are a phenomenon of correlated growth during development of humerus and musculo-spiral nerve in the first place, somewhat exaggerated by the shortness of the shaft and the form of the unspecialised articular ends, and, possibly, later, by the related deltoid insertion in the second place. That the spiral groove of the adult

humerus is so much broader than the structures lying in it is merely an indication of the early date of its production, when the girth of the nerve relative to the length of the bone was much greater and separated the origin of the two humeral heads of the triceps at the time when they were acquiring a firm attachment to the ossifying tissue of the shaft; for muscles never attach themselves to cartilage, but only to the perichondrial membrane, which is later incorporated with the periphery of the bone. The causation of the spiral groove of the humerus has no relation to the torsions about to be considered.

The changes of torsion and angulation of the articular ends which take place between the 20-mm. and the 30-mm. stages are attributable in the case of the upper extremity to the pre- and postnatal alteration of position of the scapula, relative both to the axis of the humerus and to the curve of the chest wall; in the one case the change is an approach of the axillary border of the scapula to the humerus, and in the other it is a change due to the increase in length and curvature of the ribs, causing the scapula to migrate towards the vertebræ and the head of the humerus to rotate inwards to accommodate itself to the altered aspect of the glenoid. The alteration in the inclination of the distal articular surfaces to the axis of the shaft is productive of the specialisation of the elbow-joint for pronation and supination of the forearm bones. Lewis, in Keibel and Mall's *Text-book*, p. 380, states that in an 11-mm. embryo, the forearm is midway between pronation and supination. This statement is incorrect, in principle and in detail, for, almost up to the 20-mm. stage, pronation and supination as movements or as postures are out of the question, owing to the form of the distal extremity of the humerus, the details of the skeleton showing that the forearm bones are parallel and the hand apparently fully supine if the plane of the hand be projected upon the plane of the lower end of the humerus; the right-angled elbow, parallel forearm bones, and paddle-postured hand make an exact reproduction of the palæo-reptilian fore-limb. The sex difference which is characteristic of the limb in the adult would seem to rest upon a less degree of specialisation of the upper extremity in the female than in the male, resulting in the greater "carrying angle" of the female. The correlation (if it be one) of this inferior grade of specialisation in the female upper limb with a higher grade of specialisation in the female pelvis is an interesting paradox.

The radius and ulna have been almost sufficiently discussed in connexion with the distal extremity of the humerus; it only remains to add that, if the inclination of forearm to arm be a true sex characteristic, the differential torsion of the two extremities of the ulna and the relative aspects of the articular surfaces of the radius should, if made capable of convenient

measurement, prove a valuable means for determination of sex in osteology and anthropology.

The Carpus and Hand.—The presence of a centrale in Model II. and the mode of its inclusion are not in agreement with the observations of Graefenberg. Graefenberg's material seemingly did not include a stage as early as that of Model I., in which no centrale is to be found, for he states that it is among those carpal elements earliest differentiated, and, further, that it is probably broken up by the appearance of the lunar, and finally disappears, leaving no trace. As against these statements I have to place the facts that the centrale is unrepresented in my 20-mm. stage, yet in my 30-mm. stage it is visible on both ventral and dorsal aspects of the carpus, where it is entirely separated from all other elements by a distinct perichondrium, and that in the depth of the massed elements it is structurally continuous with the naviculare through a faintly staining cartilaginous layer (fig. 9). This further confirms Owen's and Mivart's views on the fate of the centrale, whilst opposing those of Rosenberg and Thilenius, and partially also those of Leboucq. The isolation of the trapezium on the radial side of the carpus has been noted in description of Model I.; its position confirms the observation of Hagen, one which Graefenberg professes to be unable to understand, in that it is practically confined to the ventral aspect of the wrist.

The question of the relation of intermedium and discus articularis cannot be fully entered into here because of the limited amount of material under discussion, but the appearance of a separate cartilaginous nodule in the 20-mm. stage, embedded in a mass of thickly crowded cells, and the absence of such an element in the later stage, which shows chondrification of the cell-mass in continuity, on the one side, with the ulnar styloid, and, on the other, with the inner edge of the extremity of the radius, both seem to indicate early differentiation of an intermedium, followed by its disappearance and replacement by the discus.

Summary of Conclusions.

Technical.

1. The first and perhaps the most critical matter, in its bearing upon the technical results of this work, is the imperative necessity, in preparing a reconstruction of the cartilaginous skeleton, to adhere slavishly, in the drawings made, to the periphery of the fully differentiated cartilage and to exclude all the surrounding transitional perichondrial tissue.

2. The second conclusion of a technical kind follows from the first, and is, that reconstructions of the developing skeleton, at stages earlier than the

"optimum" of cartilaginous development, must necessarily be ambiguous since the zones of transition are much wider and more difficult of limitation, whilst the shape of the growing chondral nuclei signifies nothing of a more than ontogenetic importance. It is not desired to convey by this that the form of the condensed blastemal skeleton suffers under the same disability for comparative purposes, quite the contrary; the blastematous stage, also, has an "optimum" development, only one which is more difficult to assess than is that of the cartilage; it probably lies in or around the immediately prechondral period. It is further desirable to emphasise that nothing in these conclusions can apply to elements which manifest anything in the nature of direct ossification, that is to say, which, among vertebrates, may ossify otherwise than through the intermediation of cartilage; for example, a drawing and reconstruction of such an element as the chondral clavicle will convey nothing of value, because the chondrification of the clavicle never reaches an "optimum" in the accepted sense.

3. The blastema stage of the shoulder skeleton represents in its massive cell agglomeration two arches, one mesial, consisting of the precursors of the supraspinous portion of the scapula and the cell-strand connecting this with the clavicle at the junction of its sternal and acromial segments, and one lateral, representing the acromion and acromial segment of the clavicle, both having comparable though simpler bony representatives in the Edentate *Cholœpus Hoffmannii*. In the absence of the clavicle of their progenitors the Cetacea show a conversion of the dorsal pillar of the medial arch into prescapula.

4. The supraspinous portion of the scapula may possibly be the original scapula of phylogeny; it certainly is a separate morphological constituent of the scapula, as evidenced by the course of its development in man and by the various forms of its equivalent in the Cetaceans cited.

5. The formation and precocious ossification of the spine of the scapula begins in cells which, appearing at the root of the prescapula, grow on to the dorsum along the coraco-scapular junction and under the trapezius-deltoid intersection, cells which are therefore intimately related to the mesial arch, and may be, like this, representative of the reptilian clavicle. Spine and acromion are joined up through the intermediation of these cells, and the junctional proliferation may be so marked as to result, under ossification, in the production of a metacromion, as in certain rodents, and markedly in the elephant.

6. The spiral groove of the humerus is due to the impress of the musculo-spiral nerve and is not due to torsion, which, however, is not absent during the growth of the cartilage, but affects only the proximal end.

7. The specialisation of the distal articular surfaces of the humerus takes place within the stages examined, and its degree is different in the two sexes.

8. The carpal centrale is most fully developed in cartilage about the "optimum" period for the other carpal cartilages. It fuses with the navicular.

9. The intermedium is present in the 20-mm. stage, and disappears before the 30-mm. stage to make way for the chondrification of the articular disc from its ulnar and radial extremities.

ACKNOWLEDGMENTS.

I desire to record my thanks to Professor W. Wright for the kindly interest with which he has followed the completion of this work; to Professor A. C. Geddes, firstly, for the use of apparatus for reconstruction, which was his private property, and, secondly, for the advice which, when in any difficulty, I could always fall back upon with benefit.

The publication has been carried out with the help of a grant from the Research Fund of the London Hospital Medical College; the drawings are by Mr W. Thornton Shiells; in the photography I have been much assisted by Mr T. Collyer Summers.

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ON THE TOPOGRAPHY OF THE INTRA-CARDIAC GANGLIA OF THE RAT'S HEART.

By JEAN MEIKLEJOHN, *John Lucas Walker Student (Cambridge).* (*From the Royal College of Physicians' Laboratory, Edinburgh.*)[1]

INTRODUCTORY.

LARGE numbers of ganglion cells and of ganglia have been described in close relation with the sino-auricular node and the auriculo-ventricular node and bundle.

I have tried to work out more fully the relations and grouping of these ganglion cells in the rat's heart. While adding little to actual facts already observed, this paper is an attempt to show these facts more definitely and to point out their relation to experimental observations.

The figures are from a single rat's heart, but the results shown by them may be taken as generally representative—they have been confirmed in the main in a large number of hearts, both rats' hearts and those of guinea-pigs, cats, and monkeys, and in the human heart.

HISTORICAL.

In 1899, Schwartz (1) published an account of the distribution of the cardiac ganglia, based chiefly on observations on the rat's heart. He describes the ganglia as lying chiefly in an area in the posterior auricular wall, bounded on the sides by the auricular appendices, and below by the sulcus coronarius transversus, in which the lowermost ganglia lie. He describes the characters of the ganglia and of individual cells, but does not show any relation with the auriculo-ventricular node which had been previously described by Kent and His.

In 1909, Aschoff (2) stated that the ganglia in the human heart lie chiefly in the posterior coronary groove, the posterior walls of both auricles, chiefly the left, sub-epicardially in a region corresponding to the original cross part of the sinus, further in the septum atriorum as far as the atrio-ventricular node, and in the heart muscle covering the

[1] This work was done during the tenure of a Carnegie Fellowship, and I have also to acknowledge a grant from the Carnegie Trust towards the expenses of publishing.

end part of the vena cava superior, and in the neighbourhood of the sino-auricular node.

Fahr (3) in 1910, in a paper on the topography of the ganglia of the human heart, states that the ganglia are most numerous where the heart nerves enter the auricular septum, round the entrance of both venæ cavæ, especially near the sino-auricular node; that a mass lies in the inter-auricular septum from which chains extend to the right auricular appendix, and downwards in the posterior coronary sulcus to the junction of the upper and middle thirds of the ventricle. The ganglia are sub-epicardial, except in the upper part of the inter-auricular septum and at the coronary sinus where they approach the atrio-ventricular node. He states that there is another chain extending downwards from between the aorta and pulmonary artery to the anterior coronary sulcus. He points out the connexion between the ganglia and the sino-auricular and auricular nodes.

In 1911, Eiger (4) published a monograph on the topography of the intra-cardiac ganglia. I have not been able to consult this paper at first hand, and rely on an abstract in the *Zentr. für Herz. u. Gefäss. Erkrankheiten*, 1912. The observations were made on human hearts and on those of guinea-pigs and mice. The ganglia in all were found chiefly in the posterior wall of the right auricle, less numerous in the inter-auricular septum and the sulcus circularis and at the junction of both venæ cavæ. No ganglia were found in the ventricles in mouse or guinea-pig. The upper part of the ventricle of the human heart contained ganglia, variable as to number and distribution. All ganglia were found sub-epicardially, none in the myocardium.

Methods and General Description of Figures.

The figures are all outlines taken from sections of a single rat's heart. The sections were cut in paraffin, serially, 5μ thick, and between each section figured there is an interval of 20 such sections. The stain used was Van Gieson's hæmotoxylin and picro-fuchsin stain, which shows the nerve cells very clearly, as well as their relation to muscle of different types. The larger nerve bundles were also well shown and could be traced through the series.

The outlines were made by means of a mirror projection with a low power. The smaller ganglia and the nerves were filled in from direct observations with Leitz oc. 1, obj. 3. No attempt has been made to figure more than the position and relative size of ganglia, and the position and direction of nerve strands.

Results.

The ganglia divide themselves chiefly into two groups.

(1) A right-sided group, which lies high up and round the superior vena cava and in close relation with the sino-auricular node. This group appears in figs. 1–11. It is a small group, densest at figs. 8 and 9. It is entirely confined to the right side of the heart, although at figs. 8, 9, 10, and 11 it is seen to communicate with the ganglia of the left side. It extends from a little distance above the sino-auricular node to a little below it, and sends fibres into it.[1]

(2) A left-sided group. This is a much larger and more scattered group, but it also is quite definite in its relations. It is shown in figs. 6–17. It is a long chain of ganglia, densest at the level of figs. 14 and 15, and surrounds the left auricle, lying in its external walls and in the inter-auricular septum. It is not continuous, but the cell groups are linked together by strands of fibres. It extends through the greater part of the auricular wall, beginning above at the level of the sino-auricular node and extending nearly to the level of the upper part of the auriculo-ventricular node. It is clearly seen to receive fibres from the cardiac nerves (figs. 10, 11, and 15). Although these entering nerves have not been traced to their source, they correspond in position to the point of entrance of the left vagus. From the ganglionic chain large strands of fibres pass downwards, which, running in the inter-auricular septum, enter the auriculo-ventricular node or run alongside of the bundle (figs. 17–33). Many of these strands contain nerve cells (figs. 18, 19, 20, and 22).

There are also several small scattered groups of nerve cells. First, a number of small ganglia, usually 2- or 3-celled, round the pulmonary artery and high up in the roof of the left auricle, which do not seem to belong to either of the groups described above nor to have any continuity with one another (figs. 1–5). Secondly, there are a few ganglion cells around the entrance of the vena cava inferior (figs. 17 and 19). No ganglia were found in the ventricles in the rat.

The ganglia therefore fall into two main groups: one high up, on the right side, and closely connected with the sino-auricular node. The other rather lower, on the left side, and connected by means of nerve strands with the auriculo-ventricular node. The experimental work of Cohn (5) showed that the right vagus acts chiefly on the auricles, while the left acts chiefly on the ventricles and through the auriculo-ventricular system. In his experiments on the dog, stimulation of the right vagus pro-

[1] These nerves break up in the node and form fine plexuses round the muscle fibres. The fine terminations are not shown here (7).

duced stoppage of the whole heart with no disturbance of the normal sequence, while stimulation of the left vagus caused less effect on auricular rate, but resulted in various degrees of block. Gauter and Zahn (6) have recently confirmed Cohn's observations, and have further defined the points of vagus action as in the nodes, for they found that vagus inhibition could be abolished by heating the node which had been affected by vagus stimulation.

The fact that there is a distinct right- and left-sided distribution of ganglia, that the right is in relation with the sino-auricular node, while the left is in relation with the auriculo-ventricular node, gives an anatomical basis for the experimental findings, since these ganglia are most probably, at least in part, terminal ganglia on the course of vagus fibres, and controlling centres for the sino-auricular and auriculo-ventricular nodes. The subject requires fuller investigation, and further observations are being made.

In conclusion, I wish to express my indebtedness to Professor Jas. Ritchie, under whose supervision this work was done, as well as to the Carnegie Trust for a grant towards the expenses of publishing.

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[Plates.

In all figures :—

P.A. = pulmonary artery.
Ao. = aorta.
P.V. = pulmonary veins.
S.V.C. = superior vena cava.
I.V.C. = inferior vena cava.
L.A. = left auricle.
R.A. = right auricle.
L.V. = left ventricle.
R.V. = right ventricle.
C.A. = conus arteriosus.
v. = ventricular muscle (the limits indicated by dotted line).

The nodal tissue (sino-auricular node and auriculo-ventricular node and bundle) is indicated in red.

Ganglia shown thus

Nerves in cross section thus

Nerves in longitudinal section thus

All the figures are projection outline drawings at a low power of sections from a single rat's heart. The position of nodal tissue and nerve elements has been filled in under a rather higher power. It is intended to represent only the position, relations, and relative size of the ganglia and nerve strands. The drawings are partially diagrammatic, but are exact within the limits stated.

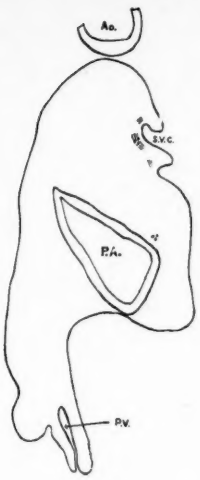

FIG. 1.

FIG. 2.

FIG. 3.

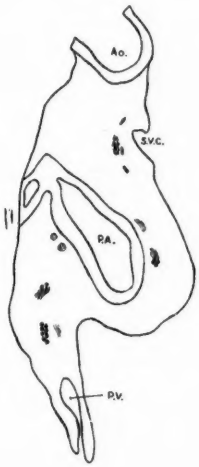

FIG. 4.

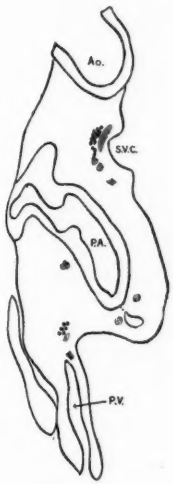

FIG. 5.

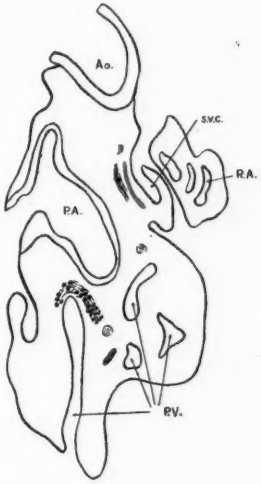

FIG. 6.

FIG. 1.—Section through pulmonary artery, aorta, and terminations of superior vena cava, and of one of pulmonary veins ; commencement of small right-sided ganglionic chain.

FIG. 2.—Section just above roof of left auricle ; right chain as above ; scattered ganglia round pulmonary artery and on roof of left auricle.

FIG. 3.—Section just above sino-auricular node ; right chain ; ganglia in roof of left auricle ; nerves round pulmonary artery.

FIG. 4.—Section through upper part of sino-auricular node ; small ganglion lying beside the node ; scattered ganglia round pulmonary artery and in roof of left auricle.

FIG. 5.—Section a little lower than fig. 4 ; nerves as in fig. 4.

FIG. 6.—Section through roof of left auricle ; sino-auricular node and upper part of right auricular appendix ; right-sided chain ; commencement of larger left-sided chain round bases of pulmonary veins.

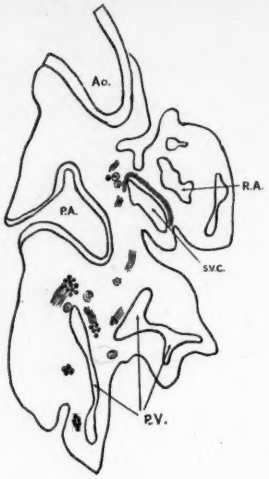

FIG. 7.

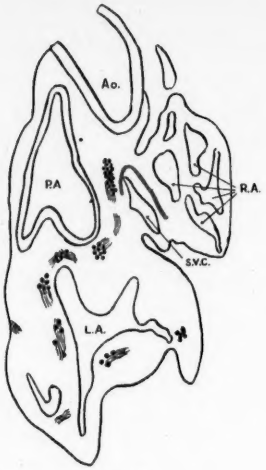

FIG. 8.

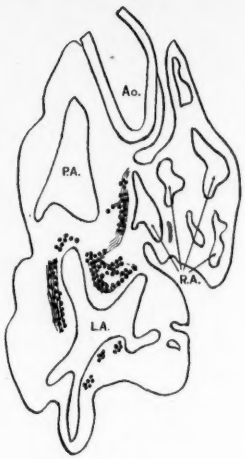

FIG. 9.

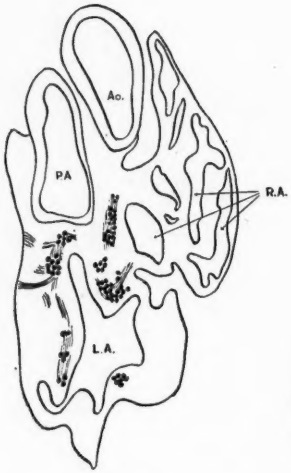

FIG. 10.

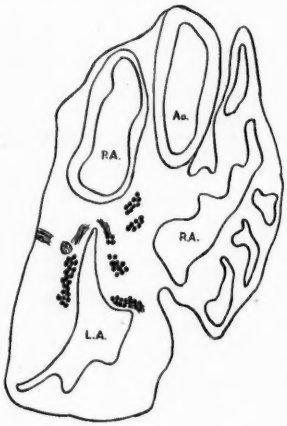

FIG. 11.

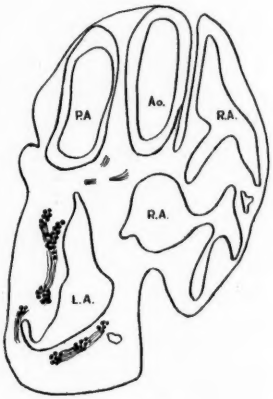

FIG. 12.

FIG. 7.—Nerve chain between ganglia near sino-auricular node; scattered ganglia of left chain round openings of pulmonary veins.

FIG. 8.—Large ganglion of right side lying beside sino-auricular node, showing connexions with ganglia of left side in wall of left auricle.

FIG. 9.—Lowest part of sino-auricular node and large ganglion of right side connected with the large ganglionic collection of left side lying between right and left auricles.

FIG. 10.—Level of entrance of left cardiac nerves; fibres seen entering on left of diagram to join left chain; lowest part of right chain below sino-auricular node.

FIG. 11.—A few nerve fibres entering on left to join left chain; the left chain is passing posteriorly round left auricle; the ganglia between right auricle and pulmonary artery belong to right chain.

FIG. 12.—The left chain has passed still further to the back.

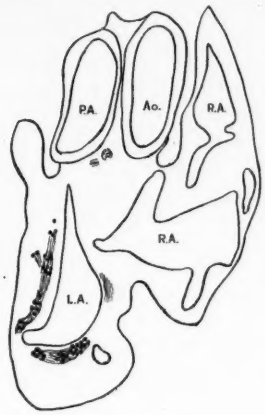

FIG. 13.

FIG. 14.

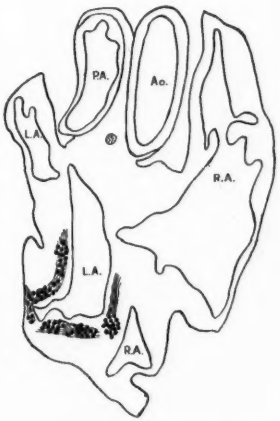

FIG. 15.

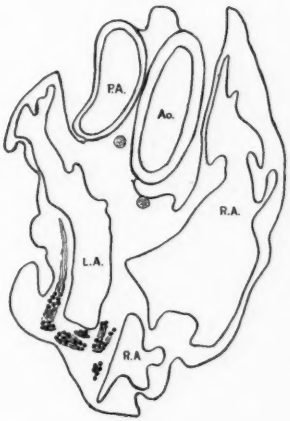

FIG. 16.

FIG. 13.—Left-sided chain passing round the back of left auricle to reach the inter-auricular septum.
FIG. 14.—Left-sided chain lying towards the back of the heart, and sending fibres into the inter-auricular septum and to the left auricular appendix.
FIG. 15.—Ganglia of left side as in fig. 14, passing down in inter-auricular septum (the nerve between pulmonary artery and aorta passes down into the ventricles in the anterior coronary groove).
FIG. 16.—Ganglia of left chain as in figs. 14 and 15.

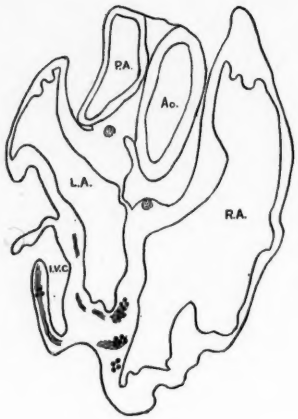

FIG. 17.

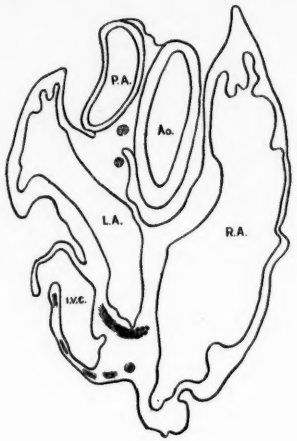

FIG. 18.

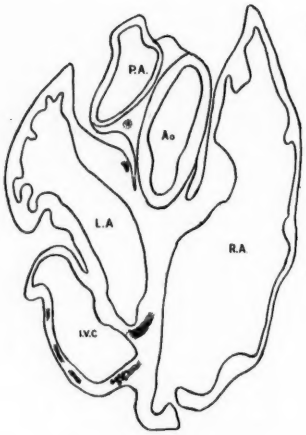

FIG. 19.

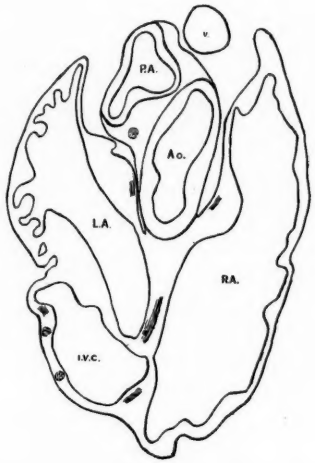

FIG. 20.

FIG. 17.—Left-sided chain passing down in inter-auricular septum ; the inferior vena cava is shown with a ganglion and fibres in its wall.

FIG. 18.—Ganglia and nerves as in fig. 17.

FIG. 19.—Nerve strand containing cells passing downward in inter-auricular septum ; nerve strands and ganglia round inferior vena cava.

FIG. 20.—Nerves as in fig. 19 (small v. in this and succeeding figures indicates ventricular muscle, the limits of which are mapped out by dotted lines).

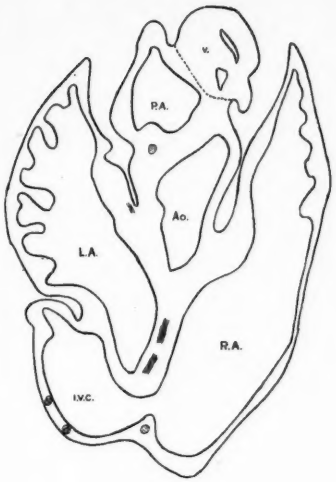

FIG. 21.

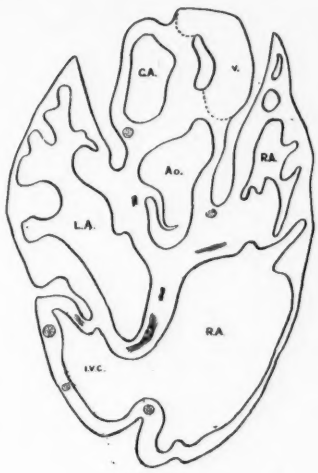

FIG. 22.

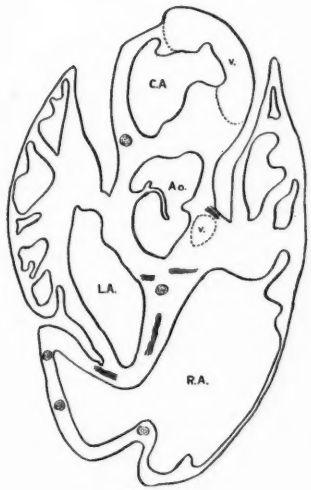

FIG. 23.

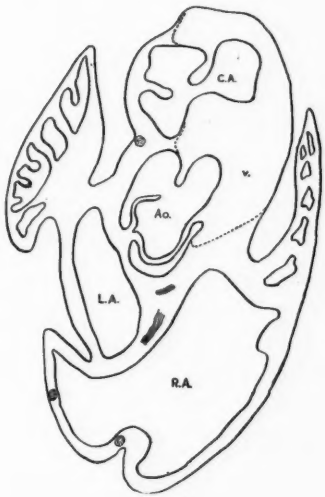

FIG. 24.

FIG. 21.—Just above level of auriculo-ventricular node ; fibres from left-sided chain passing down in inter-auricular septum and right auricular wall (some of the latter pass lower to auriculo-ventricular bundle ; some pass to ventricles in the posterior coronary groove).

FIG. 22.—Upper part of auriculo-ventricular node ; nerve with cells passing to the node.

FIG. 23.—Level of auriculo-ventricular node ; fibres passing to the node and downwards in right auricular wall from left chain.

FIG. 24.—Level of auriculo-ventricular node ; nerve fibres as in fig. 23.

FIG. 25.

FIG. 26.

FIG. 27.

FIG. 25.—Level of auriculo-ventricular bundle ; numerous nerves passing forward to the bundle in the inter-auricular septum.

FIG. 26.—Level of auriculo-ventricular bundle ; nerves running forward to the bundle and accompanying it (these nerves enter and break up in the bundle).

FIG. 27.—Bifurcation of the bundle ; nerves accompanying it shown in cross section.

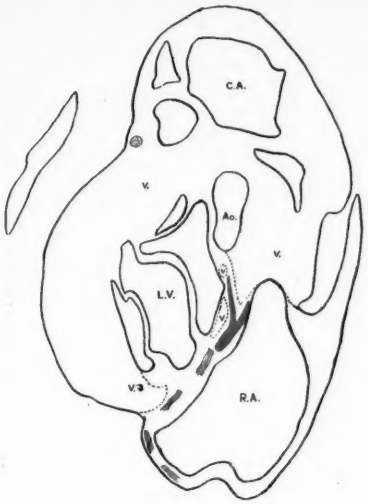

FIG. 28.

FIG. 29.

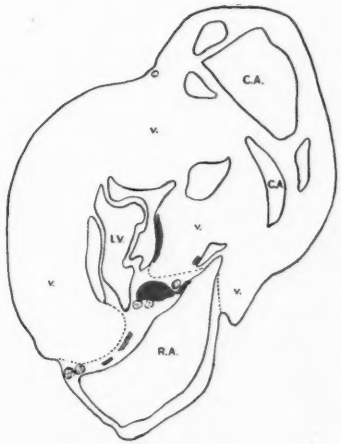

FIG. 30.

FIG. 28.—Bifurcation of the bundle ; nerves running in inter-auricular septum to join it.
FIG. 29.—The bundle has divided into right and left branches, but main stem still shown owing to sections being oblique to its course ; nerves accompanying it ; one shown with right branch.
FIG. 30.—Main stem and branches of bundle and nerves accompanying the bundle.

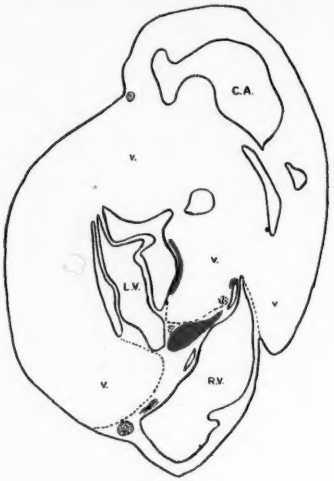

FIG. 31.

FIG. 32.

FIG. 33.

FIG. 31.—Main stem and branches of bundle ; the branches have passed well to the right and left of the septum, and their nerves have broken up in them ; two larger nerve strands shown with main bundle.

FIG. 32.—Right and left branches of bundle and main stem accompanied by nerve strand.

FIG. 33.—Right and left branches of auriculo-ventricular bundle ; no nerves shown accompanying the branches, as they have entered and broken up in them ; nerve in anterior coronary groove is derived from right-sided chain ; that in posterior groove from left chain.

THE SECOND VISCERAL ARCH AND GROOVE IN THE TUBO-TYMPANIC REGION.

By J. Ernest Frazer, *Lecturer on Anatomy in the Medical School of St Mary's Hospital.*

In 1910 I brought the results of an investigation into the development of the naso-pharynx before the Anatomical Section of the British Medical Association, calling attention at the same time to the fact that the tubo-tympanic recess has in its floor the outer ends of the first two arches and grooves, and that consequently its posterior margin or wall is formed by tissues owning a third arch value: further, I showed that the first and second lateral pouches persisted and were recognisable throughout the second and third months, with the outer ends of the arches, whereas the inner portion of the second arch disappeared in the tubal region, the wall of the cavity in its neighbourhood undergoing what I called—in default of a better term—a process of atrophy. The description which I published at that time (*B.M.J.*, 15th October) was rather of the nature of a side-issue in the work on which I was engaged, and no subsequent reference was made by me to it; but in the present paper I hope to give a more complete account of the modifications which occur in this region and affect the second arch in particular, and to indicate the rearrangement of the parts that leads to the ultimate formation of the tubo-tympanic cavity.

Before entering on such a description, it is perhaps advisable to lay a little stress on the general characters and relations of the tubo-tympanic recess. The early pharynx is a cavity that is very wide from side to side in front, and narrows rapidly and considerably as it is traced back towards the stomach; it is flattened dorso-ventrally, so that the floor and roof are almost in contact, perhaps quite in contact in the living embryo. It has no proper side wall, the lateral limits of the cavity being made by the junctions of floor and roof, and the visceral arches and grooves are only found in the floor; the grooves terminate in lateral pouches (whose sub-divisions do not affect the general arrangement), and these lie therefore in the region of the lateral parts of the cavity, where they form depressions deeper than the remainders of their corresponding grooves. Towards the end of the first month the narrowing of the cavity from side to side is seen to take place less gradually than in the earlier stages, and the region of the third arch is the level at which this more sudden decrease in width is placed, so that in front of this arch there remains a wide area, and the

part of the cavity that extends out in front of the arch, beyond the general lateral limits of the cavity, constitutes the tubo-tympanic recess that will subsequently be moulded into the cavity of the middle ear and Eustachian tube.

Fig. 1 gives in outline the shape of the pharyngeal cavity in a 12-mm. embryo, and illustrates this description, showing how each broad and open recess is floored by the outer parts of the first two arches, how their grooves lie behind them and end externally in deeper lateral pouches, and how the third arch, lying between the second and third pouches, necessarily forms the short posterior boundary of the recess.

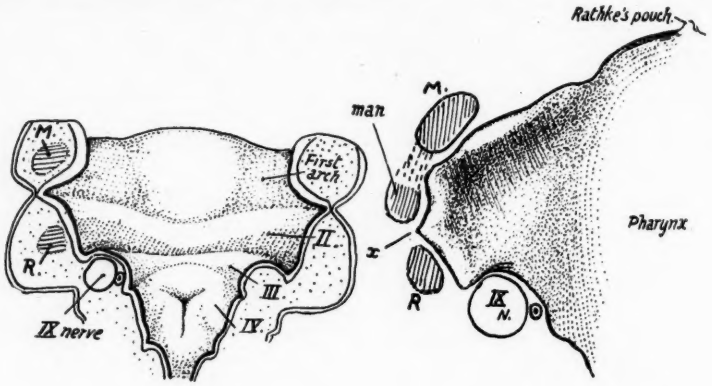

FIG. 1.—From models to show (A) floor of 12-mm. pharynx, (B) view from above of left tubo-tympanic recess in 16-mm. embryo. Somewhat diagrammatic.

M., R., condensations forming Meckel's and Reichert's bars respectively; *man.*, position of manubrial extension from first arch. This causes depression of the neighbouring wall, with a secondary projection, *x*, behind it.

Later, as the recess elongates obliquely and develops, it is rotated on its longitudinal axis so that its original floor becomes its front and outer wall, and the periotic capsule that primarily lies on its roof assumes an inner and posterior relationship to it.

It follows from the foregoing statements that an account of the arches utilised in the formation of the recess must concern itself mainly with the floor, and that, as development proceeds, the arch-structures which persist will be found in association with what is described as the outer wall in the anatomy of the adult.

The second drawing in fig. 1 is an outline of the cavity seen from above in the 16-mm. embryo, and the projections of the first and second lateral pouches are easily recognised and compared with those in the 12-mm.

specimen. In the older one, however, the wall of the cavity has been pushed in immediately behind the first pouch by the extension of a mass of condensed mesenchyme from the upper part of the first arch, concerned in forming the handle of the malleus, etc. This incursion is associated

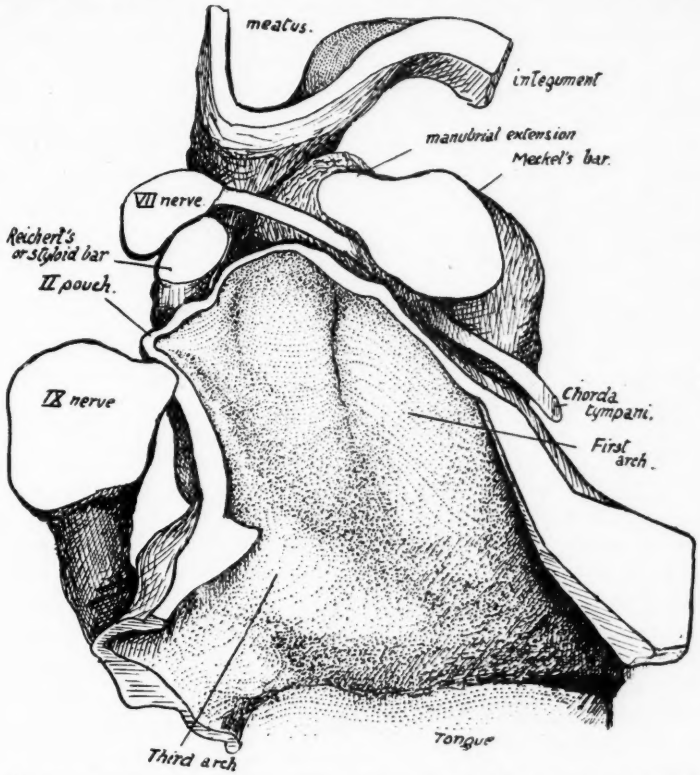

FIG. 2.—Floor of left recess, roof removed. From model (magn. $100 \times \frac{5}{6}$). A portion of the margin of the tongue is seen below. 16 mm.

with temporary separation of the pouch from the ectoderm (see figure), and also with the formation of a secondary projection in the margin of the cavity just behind the portion pushed in by the manubrial condensation.

On removing the roof of the recess and thus exposing the floor, the disposition of the arches becomes apparent. Fig. 2 is a drawing of the floor of the left recess in an embryo of 16 mm. exposed in this way, and is

of interest because the key to subsequent changes is to be found in the conditions present at this stage.

The front part of the field is formed by structures of the first arch, among them Meckel's bar passing downwards and inwards, and behind this a deep but narrow sulcus marks the situation of the first visceral groove ending externally in the first lateral pouch, just above which the chorda tympani runs forward. The second lateral pouch is apparent behind the styloid bar (Reichert's bar), between this and the glossopharyngeal, which is closely applied to the wall of the recess here: this is the definite position of the second pouch, shown also in fig. 1 in the 12-mm. specimen, and is the position maintained by it until the growth of the cartilaginous auditory capsule effects a separation between it and the nerve.

The area of the second arch lies between the first and second pouches, and is plainly subdivided into two districts, an anterior one showing the prominence caused by the underlying manubrial condensation, and a posterior one exhibiting a convexity which is evidently caused by the styloid bar against which this part of the floor rests; the sulcus between these two districts corresponds, of course, with the secondary projection seen externally in fig. 1.

But, if we follow the complete second arch area inwards, it becomes clear that there is already a difference apparent between the arrangement of structures in the floor here and that in the 12-mm. embryo, and this difference is due to growth of the third arch tissues. The region of the third arch, where it forms the hinder boundary of the recess, has become more prominent, and an extension forward from it has taken place, spreading across the inner part of the floor towards the first arch, and, in doing so, covering over the tissues of the second arch in this situation, so that this latter is not represented in this part of the floor. The extension of the third arch is evident in the figure, and it is seen to be separated from the first arch region by a shallow gutter towards which the limiting sulci of the second arch are directed: they reach a broader hollow from which the first-mentioned shallow gutter is directed forwards and inwards. The floor of the gutter and broader hollow, as seen in the model and the drawing, is composed of much-thickened epithelium, and a reconstruction of the regions with the epithelium removed allows the surface appearance of the second arch to be followed a little lower than in the complete condition; but the general result is the same—the outer part of the arch is concerned in the formation of the floor of the cavity and is divisible there into its two districts, but the inner part has dropped out of the floor, and is separated from the cavity by a forward growth of the arch immediately succeeding it.

It may be pointed out here that the floor of the recess shows a general and well-marked concavity from before backwards as well as from without inwards, a condition that is not brought out in the drawing owing to the necessity for a clear presentation of the arches, etc. In other words, the growth of the first arch has turned up the related floor, the same effect has been produced on the manubrial district of the second arch by the mesenchymal extension underlying it, the styloid bar is directed downwards as well as inwards, so that the posterior district of the arch is correspondingly disposed, and the third arch is raising the hinder part of the floor as a result of its increasing size: the part that remains unaffected by these several factors is the broad hollow toward which the other surfaces slope, and the narrower gutter leading away from it which marks the place where the first and third arches have not yet met, but where such meeting is about to occur.

The further development of the region up to the third month is a simple progression of the changes seen in their early stages in fig. 2. The first arch area stands up more, the manubrial district of the second arch is more prominent and defined, and the second pouch is recognisable between the styloid bar and the glosso-pharyngeal nerve. But a distinct change is visible when attention is directed to the third arch region; the arch, presumably as a result of its growth, is encroaching on the lumen of the inner portion of the cavity from behind, so that already some indication of a division into tubal and tympanic parts is foreshadowed. A drawing of one of the models showing this stage is seen in fig. 3, and it is interesting to compare it with the earlier condition: recognition of the first and second arch region is easy, and the districts into which the latter is subdivided are evident and unmistakable.

But equally evident and unmistakable is the change that is apparent in the back and inner boundary of the recess. The third arch has grown and has carried this part of the hinder wall in a forward direction, tending to lessen the size of the opening of the recess from behind forwards: this can be graphically demonstrated and appreciated by superimposing a tracing of the later upon the earlier stage, when the first and second arch areas will be found practically to correspond and occupy their proper positions, whereas the increased obliquity forward of the hinder wall shows at once how much this part has extended in a forward direction relative to the other parts. Such growth, moreover, is most marked at the inner or pharyngeal end of the hinder wall, so that the corresponding portion of the recess exhibits some narrowing compared with the remainder.

The chief growth appears to be in the prominent part of the arch from which (fig. 2) the forward extension takes place, and in this extension

itself. As a result of growth in the first-mentioned region, the depth and abruptness of the postero-internal wall of the broad hollow in the floor is increased and the hollow thus accentuated, while the growth of the forward extension has enabled this to reach the mandibular arch and to obliterate in doing so the gutter that separated the two in the earlier stage. The whole process is a continuation of that seen in its early stages at 16 mm.,

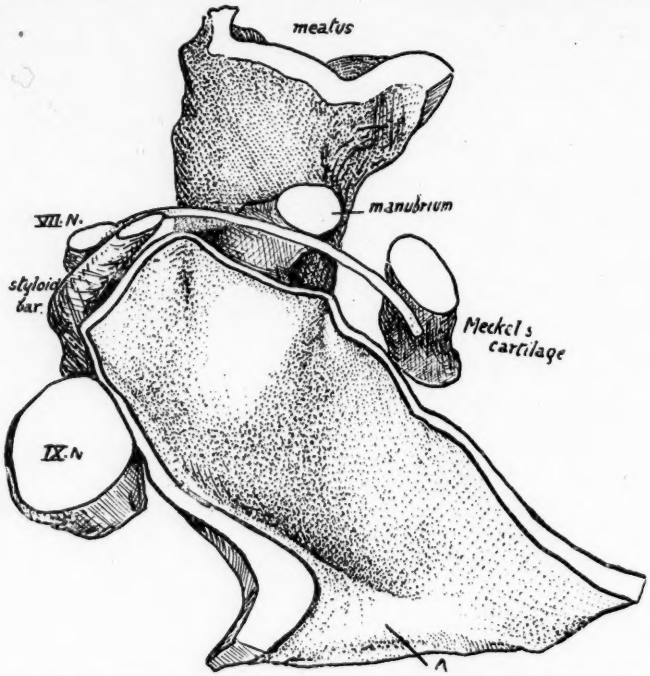

FIG. 3.—Left recess, from a model. 27 mm. Observe that the forward extension, A, from third arch along the floor is much more marked and prominent than in the last figure, and has reached the first arch.

and indicates the results of growth forward of the third toward the first arch across those tissues of the second arch which should be in the inner part of the floor of the recess, but still leaving the outer parts of the second arch exposed in the corresponding portion of the floor.

The two districts into which the outer part of the second arch is divided are more definite at this stage, principally because of the greater prominence and definition of the manubrial swelling, which not only stands out into the cavity, but has a deeper sulcus between it and the styloid district; at

one place this sulcus shows an extension deeply round the back of the manubrium, which is apparently an early indication of the posterior recess of Tröltsch. The styloid district is if anything relatively smaller, depending on the thickness of the bar on which it is moulded. The second pouch is seen behind, and a little internal to, the styloid district, between the styloid bar and the glosso-pharyngeal nerve.

The first arch region, like the manubrial mass, stands up more than in the early stages; in other words, the front and outer part of the floor is being lifted up by underlying growth, and thus being brought more into the position of an outer and front wall, as mentioned in the beginning of

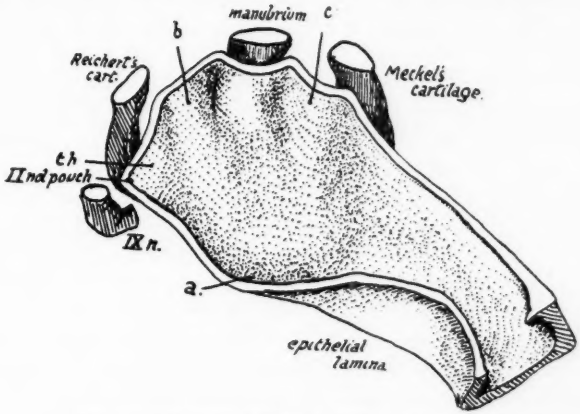

FIG. 4.—Left recess, simplified, from model. 35 mm.

a, bottom of tympanum practically corresponding with lower extremity of meatal plate and tympanic ring; *b*, *c*, prominences made by back and front edges of meatal plate growing in round the manubrium; *th.*, tympano-hyal area.

this paper. It follows as a result that the growth of these parts assists in accentuating the hollow that lies at the bottom of their declivities.

It is about this time that the process begins, the effects of which are so strikingly seen in specimens of about 35 mm. length: apparently the mass of the third arch advances toward the area of the first arch with greater rapidity, along the floor, so that one is heaped up, so to speak, against the other, with an epithelial septum lying between them composed of the cells which at the time cover their meeting surfaces.

Fig. 4 is from a model of a 35-mm. embryo, and shows how greatly the third arch has extended forward; comparison with the earlier stages makes this evident. The recess as a whole is slightly longer, and the growth of the third arch particularly affects the inner part and narrows it, thus

definitely indicating the distinction between tube and tympanum. But it is equally plain that this narrowing has not been obtained by a raising up of the epithelial floor as a result of growth under it, but by a fusion of the surfaces of the first and third arches where they have come into contact; for an epithelial lamina is present below the newly made "floor" in this region which is continuous with the epithelial lining of the cavity along its length from the hinder boundary of the pharyngeal opening to the hollow situated at the foot of the anterior district of the second arch in the tympanic region. Such a lamina can be nothing but the covering of the prominent arches caught between them as they meet. The lamina, as shown in the model, consists only of a solid and continuous epithelial septum; but under the microscope broken layers and masses of cells can be found which are not suitable for modelling, but indicate that the fusion is more extensive behind and below than is suggested by the model. What is probably the beginning of this process is found in the 29-mm. embryo, in which an epithelial mass can be seen lying above the front part of the forward extension of the third arch, between the thicker posterior part of this extension and the first arch eminence.

The lower part of the tympanic region is now (fig. 4) more definitely limited in front, by the fusion that narrows the cavity, and it becomes necessary to see how far back the fusion would extend if it were marked out on the earlier recess shown in fig. 3. At that stage there is a large and well-marked hollow to be seen; it lies along the lower margin of the first arch area and extends back to the foot of the manubrial swelling and forward to the forward-growing process of the third arch, which separates it from the opening of the recess. In the stage shown in fig. 2 its narrower inner part forms the gutter which is interrupted by the process of the third arch, so that the hollow seen in fig. 3 includes the commencement of the gutter. This hollow, as seen in fig. 3, is obliterated by the adhesion and fusion of its postero-internal with its antero-external wall, *with the exception of the part which lies at the foot of the manubrial swelling*; this part is seen at *a* in fig. 4, the remainder of the hollow in front of this being obliterated and its adherent walls forming the epithelial lamina, which increases in depth as the area of adhesion increases. The convexity of the first arch which forms the antero-external wall of the hollow is preserved in the adherent state, and can be appreciated in the 35-mm. model, in which the epithelial lamina is concave forward and continuous with the curve of what is left of the first arch region above the area of fusion.

The growth and fusion which goes on at the inner part of the recess does not affect the outer portion of the second arch directly, but leaves it exposed in the wider part of the cavity where no fusion has occurred.

Remembering that the floor of the recess becomes the outer wall of the ultimate tympanum, it is easy to follow the changes which are apparent in the surface view of the arch that is obtained here: the changes are evident in the figures of the various stages.

In this connexion it is necessary to inquire first into the nature of the structures which are in relation with the deep or outer side of the arch seen in the floor of the recess. In the 12-mm. stage the first and second lateral pouches are in contact relation with the ectoderm of the corresponding external grooves, but after this they are separated by the increasing thickness of the mesoderm which interposes itself between the outer and inner grooves. In the case of the second pouch the separation causes at first an elongation of the epithelial connexion, drawing it out into a narrow *ductus branchialis* connected with the lining of the precervical sinus; this soon atrophies and disappears, and no trace of the structure can be found subsequently. With the first pouch, however, the case is different so far as the sequel is concerned. Possibly the mesoderm which effects the separation is the condensed mass which extends back from the upper part of the first arch to the outer side of the chorda tympani, and constitutes what I have termed the "manubrial mass" or extension in this paper. This forms a thick mass which is continuous in the sixth week with the condensation of the anlage of Meckel's bar, the continuity lying above and outside the first pouch. The mass formed in this way has therefore extended from the first arch into the second, pushes in the anterior part of this last arch to form the anterior district visible in the 16-mm. stage, and is placed between this part of the second arch in the floor of the recess and the epithelium-lined recess or bay of the external groove which represents the early state of the external meatus at this stage.

The position of the developing meatus and the shape it assumes appear to be factors of some importance in the production of modifications in the aspect of that part of the wall of the tympanum which is under consideration, and, without entering into the whole question of the formation of the meatus, it may be of some little use to give a brief account of the structures as they concern the tympanum.

The external meatus, at the stage shown in fig. 2, is represented by a broad groove directed downwards and inwards, and ending below in a pit which is placed below the level of the outer part of the tubo-tympanic recess: the structure as a whole can be described as situated obliquely below and outside the recess, and separated from it by the "manubrial mass" of cells. In fig. 2 the upper and outer part of the groove is seen cut through at the top of the drawing, and from this the floor of the groove can be followed down and in, separated from the floor of the recess by the

manubrial extension, until it is lost to sight under the floor of the recess. The upper part of the manubrial mass is thick, but it thins away below, so that the pit in which the meatal groove terminates below is nearer the floor of the tubo-tympanic recess than is the upper part of the groove, and the part of the floor with which the pit is in nearest relation is near the lower end of the anterior district of the second arch. In later stages the relative length of the open groove has decreased, while that of the pit has much increased, so that this latter is now in relation with the floor of the recess —the manubrial mass intervening—so far in as almost to reach the level of the bottom of the hollow in the floor seen in fig. 3; in other words, the

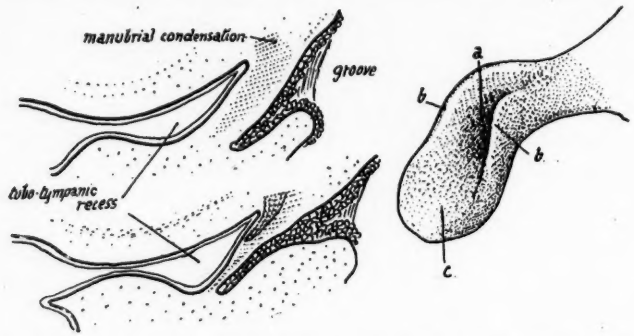

FIG. 5.—On the left, two schemes to show the relations between the recess and the meatal extension (meatal plate). Represented in transverse section. In the upper figure the plate is separated from the recess by thick condensation, but in lower figure the meatal extension is longer and more nearly in contact with the recess, with thinned out mesenchyme intervening. Note the correspondence between the extremity of plate and bottom of tympanum. The right-hand figure represents the separated meatal plate.

a, concavity receiving manubrium; *b b*, edges passing round manubrium to reach wall of recess; *c*, flat lower part applied to wall of recess below level of manubrium.

inner part of the pit-like meatal extension is now applied to the outer wall of the hollow in the recess and to the lower part of the anterior district of the arch above this, and here is separated from them only by the attenuated lower part of the "manubrial" condensation, and is consequently plate-like in form, whereas the outer and upper part of the meatal growth is further away, separated from the recess by the greater thickness of the condensation where the handle of the malleus is developing, and the edges of the meatal extension are growing out toward the recess on each side of the handle, thus limiting the condensation and fitting in between the handle and the styloid bar behind and Meckel's bar in front.

Fig. 5 shows schematically the application of the meatal extension to the floor of the recess, and in the same figure is given a sketch of the

extension to exhibit its general shape. Its inner part is a solid plate of epithelial cells—the *meatal plate*—and is practically flat at its extremity, but higher up it is concave where it receives the manubrial mass which separates it from the floor of the recess; it is at the edges of this concave portion that the growth inwards takes place towards the floor.

We can now appreciate the appearance of the floor seen in the ninth week (fig. 4). The lower end of the meatal plate is applied to the floor just above the point *a*—with, of course, a thin mesenchymal layer intervening—and above this it is applied to the floor as far up as the definite prominence caused by the handle of the malleus. Here the plate becomes separated from the floor by the thicker mass of structures, but its edges have grown forward on each side of these and have produced a decided bulging of the floor on each side of the manubrial swelling, marked in the figure as *b* and *c*. Of these, the anterior one, *c*, is evidently produced in the first arch region in front of the remains of the first groove, while the posterior one, *b*, is situated behind the secondary post-manubrial sulcus (posterior recess of Tröltsch), and therefore in the posterior district of the arch. A glance at fig. 2 will show that this posterior district is in its early state practically altogether in relation with the styloid bar, but in fig. 3 the bar is proportionately smaller; it has not kept pace in its growth with the general enlargement of the recess, and thus is only occupying a part of the field of the posterior district. It is the unoccupied area antero-external to the bar which is reached by the posterior edge of the meatal plate and is pushed in by it, and thus the part of the floor which covers the styloid bar is again and more definitely mapped out, and can now be termed the "tympano-hyal" area (*th*, fig. 4). At this stage, therefore, we can recognise the situation of many definite structures in relation with the outer wall of the tympanum. The area over which the meatal plate comes into relation with the floor of the recess determines the extent of the tympanic membrane, and this area is apparent in fig. 4; the definite swellings produced by the edges of the plate at *b* and *c* are continuous below with the indefinite convexity which covers the flatter lower end of the plate, and the whole forms a horseshoe-shaped area round the manubrial swelling that marks the position of the tympanic membrane. This area has the bony tympanic ring round its periphery; the ring does not produce any visible impression on the floor, but its lowest part comes down practically to the level of the point *a*. The chorda tympani is not shown in the drawing, but would be as in the other figures; and we can thus see that the outer wall of the tympanum, nearly if not quite up to the level of the chorda, is formed from the floor of the recess, and has both first and second arch elements in it, the share taken by the first arch being limited to the part in front of the handle of the malleus.

The area of the second arch includes the outer wall behind this, and turns on to the back wall to take in the tympano-hyal region.

The second pouch is evident between the styloid bar and the ninth nerve, which still approaches the wall of the recess here, although the growing auditory capsule is carrying it as a whole further away. Observe the position of the pouch: it is no longer behind the styloid bar as in fig. 1, but is now definitely internal to it, a position which has been gradually assumed as the recess has developed; that is to say, that the original relation, which was postero-internal, has now lost its posterior character and remains only internal. The relationship is still, of course, morphologically posterior in the sense that if we follow the side-limits of the pharynx in an aboral direction we come to the pouch after passing the arch and bar.

The outer wall of the tympanum, so far as it has been seen, appears to be fixed in its position as a result of its relations and connexions with the structures lying deep to it, and it would seem probable that, if this is so, that part of the outer wall which lies above the chorda tympani must be formed as a secondary derivative of the roof of the recess.

The limitation of the area of fusion as shown in fig. 4 strongly suggests that there is some connexion between the persistence of the non-fused tympanic region and the close relation of the ectodermal meatal plate, but what this connexion may be, if it exists directly at all, there appears to be no evidence to show. I hope to get some light on the question by examination of other forms, but in the meantime can only say that the advance and fusion with anterior structures of the third arch does not take place where the meatal plate is in relation with the floor of the recess, that the size of the cavity is consequently greater in this area, and that here the second arch remains in the floor and is not covered in, as in the more internal parts, by the forward advance of the arch-structures which lie behind it in a morphological sense.

The growth of the third arch tissues and the consequent covering over of those of the second arch where it occurs is a phenomenon which has its parallel in the external growth of the second arch that hides the third and other arches and even extends forward over the mandibular derivatives. It is interesting to observe that the second arch begins to drop out of the floor of the recess about the time that it commences to extend its muscle cells more externally away from its own special region. Before this it lies (see fig. 1) as a complete visceral bar across the pharyngeal floor, passing to the region of the future back part of the tongue; but after it has commenced its external growth the central portion apparently ceases to grow proportionately and seems to be only responsible for the formation of the fibres of the stylo-hyoid and digastric. This comparative atrophy of the greater part of the original arch leaves it poorly represented in the general floor, and it is in fact seemingly completely covered by the increased internal growth of the third

arch; the only part of the arch persisting in the floor is that outer portion which I have shown in this paper to remain as part of the floor of the recess or outer wall of the tympanum, and the stapedius is developed here from the muscle cells of the original arch-tissue. While examining sections I have found some reason to think that the attenuated second arch can be followed in its proper situation—though covered by third arch tissues—during the second month, and that the true nerve of the arch is to be found in the remnant: this must form the subject of a future investigation, but it may be mentioned here that the nerve in question appears to be the connexion running from the facial to the glosso-pharyngeal, which, in the embryo, makes its junction deeply in the basal portion of the tongue.

The increase in the pharyngeal aspect and extent of the third arch fills the deficiency resulting from the comparative atrophy of the second arch in the pharyngeal floor. This growth of the tissues of the third arch in the neighbourhood of the opening of the tubo-tympanic recess is associated with the formation of the palate. When investigating the development of the naso-pharynx and nose it was necessary to work out the development of the palate, and in 1910 I called attention to the fact that a forward growth takes place from the region of the third arch to join the (maxillary) palate-fold, and is, in fact, the basis of the pharyngeal extension of the fold. I also pointed out that the maxillary fold is really an outgrowth of the floor of the pharynx, and it can be understood, without entering further into the formation of the palate, that if the fold extends back on the floor to the hinder limit of the first arch, at the junction of the recess with the pharynx, the forward growth of the third arch will reach it when it extends across the buried remnants of the second arch. So far as I am aware, this observation and suggestion of the formation of the palate from two distinct elements was a novel one, and it interested me to find that Michio Inouyé (*Anat. Hefte*, 1912) described and figured the palate in moles and mice as developing in separated parts which coalesce later: in the human embryo, however, the two parts have always met before they produce any appreciable "backward extension" that can be seen on the pharyngeal wall.

The relative position of these extensions of the third arch can be understood by referring to the stage shown in fig. 2: the palate fold will be placed along the outer side of the sulcus beside the tongue, just internal to the forward extension from the third arch, and the palatal growth from this arch will meet it in this line. Thus, when the compound ridge becomes apparent on the surface, it stands out as a fold between the opening of the recess and the sulcus beside the tongue, dividing the original floor of the pharynx in this situation into an inner and outer portion; the former is depressed with the tongue and makes the posterior part of the wall of the mouth, but the latter is raised up, supported on the mass of mandibular mesenchyme, and becomes the antero-external wall of the tube and tympanum. We have seen that the tissues of the third arch by their extension make the "floor" of the tubal opening, and this extension is continuous with the palatal growth, so that structures developed between the opening and the palate are also formed in this extension, which covers the more central parts of the second arch; in fact, it may be shortly stated that all the structures which lie in the plane of the wall of the pharynx between the floor of the Eustachian tube and the stylo-hyoid level are derived from the secondary growth of the tissues of the third arch.

Internal to (*i.e.* below) the palatal growth the mesenchyme of the third arch

extends on to the tongue, covering over the remains of the second arch and forming a new posterior part for that organ.

At the end of the second and early part of the third month there appears to be a rapid increase of the third arch growths, so that we find about this time that the inner part of the tubo-tympanic recess is narrowed by growth of the tissues there, the palate fold becomes more prominent preliminary to closure, and the tongue extension forms a prominent mass *in sitû* which makes with its fellow an angular depression that marks the future foramen cæcum. In this way the partial fusion which brings the tubal division of the recess into evidence can be said to be associated with the later stages of formation of the palate, not as cause or effect, but as a result of the same factor, the rapid growth of the tissues of the extension forward from the third arch which has buried under it those of the inner and larger part of the second arch.

In this account of the formation of the tubo-tympanic region I have, *inter alia*, dealt rather fully with the question of the closure of part of the recess to produce the tubal portion of the cavity, because my later and more detailed investigations have led to results which call for a certain amount of modification as well as extension of the views outlined in my previous paper. In that account I termed the process an "atrophy," and in one sense the term is a true one, for there is, without doubt, an atrophy of the layer immediately lining the cavity, and a failure of development of the true second arch where it lies below this part of the cavity; but, although I had made certain observations on the palate growth, I had failed to appreciate the wide extent of the forward movement of the third arch, and was thus at a loss to account for the occurrence of the narrowing, even though I described the appearances as probably indicating that it had been preceded by epithelial adhesion between the walls. It was therefore suggested that the second arch atrophies, leaving it to be understood that when it disappears the third and first arches must of necessity come together. The present investigation, aided by a series of reconstructions of the floor of the cavity, show that that suggestion rather placed the cart before the horse—that the disappearance of the second is a result and not the cause of the changes affecting the third arch, depending, like the fusion with the first arch, on the growth of the tissues of the third arch.

This correction of a suggestion by a truer conception of the conditions involves as a corollary the modification of another and smaller point in the original description. This concerns the presence of a shallow groove emerging from the opening of the recess and situated in front of what is evidently part of the third arch: such a groove, without a right conception of the extent of growth of the third arch, suggests itself at once as a portion of the second groove, and falls into line thus with the idea of a partial atrophy of the arch in the tubal region and its reappearance further in. But although it is in front of third arch structures it is really

only a groove secondarily made between these and other tissues of the same arch, part of the forward growth, and cannot therefore be properly described as a portion of the second groove.

The second groove, however, may be said to reappear below the main mass of the growth of the third arch. This mass has been described as showing three principal processes or parts—an upper forward extension in the tubal region, a palatine part, and an extension to the tongue: the last of these is separated from the pharyngo-epiglottic fold, which is the proper third arch in the floor of the pharynx, by the deep groove in which the tonsil develops and which is part of the second visceral groove. It is true that the second arch structures in front of it are covered by those of the third arch, but the groove itself appears to remain unaltered from the 12-mm. stage, and really marks the position of the second groove. The groove first described, at the opening of the recess, may possibly mark the place where the third arch growth crosses the original situation of the second groove, but as it is on a third arch basis it ought not to be classed with the second groove, which would properly be described as reappearing below (and not above) the level of the palate-fold.

The second pouch remains in its position between the upper part of the styloid bar and the glosso-pharyngeal nerve up to the stage to which we have so far followed the development, but the fate of the second groove between the pouch and the lower part of the tympanum is not so clear. Examination of the earlier stages shows that the lower portion of the groove in this fraction of its extent is filled by proliferated epithelium, and the condition in later stages suggests that the lower portion may be obliterated: probably it would be safe to say that only the upper or outer extremity of the groove remains, along the postero-internal edge of the tympano-hyal area (fig. 4), while the lower part, extending to the bottom of the tympanum, only shows the partly obliterated remnants of the groove remaining in their proper position between structures of the second and third arches.

The second pouch is affected in the direction it assumes by the relationship of the auditory capsule to the developing recess. The capsule grows very rapidly, and, being situated above the roof of the recess, produces a concavity on the upper aspect of the roof. The pouch is at the outer and posterior part of the roof and concavity, and thus is on the whole turned somewhat upwards with reference to the general level of the roof. The condition may perhaps be rendered clearer by fig. 6, from a model of the parts in a fœtus of 50 mm.: the roof of the tubo-tympanic cavity is seen from above and behind, exhibiting the depression caused by the cartilaginous (cochlear) capsule with the second pouch turned slightly up at its

outer and posterior part. The cartilaginous structure is shown separated in part and reversed, so that the hollow into which the pouch fits is seen on it: this is the fossula rotunda. At this time there is no part that could be termed the tympanic sinus, the locality in which one would expect *a priori* to find the pouch, and if the sinus is related to the pouch it is

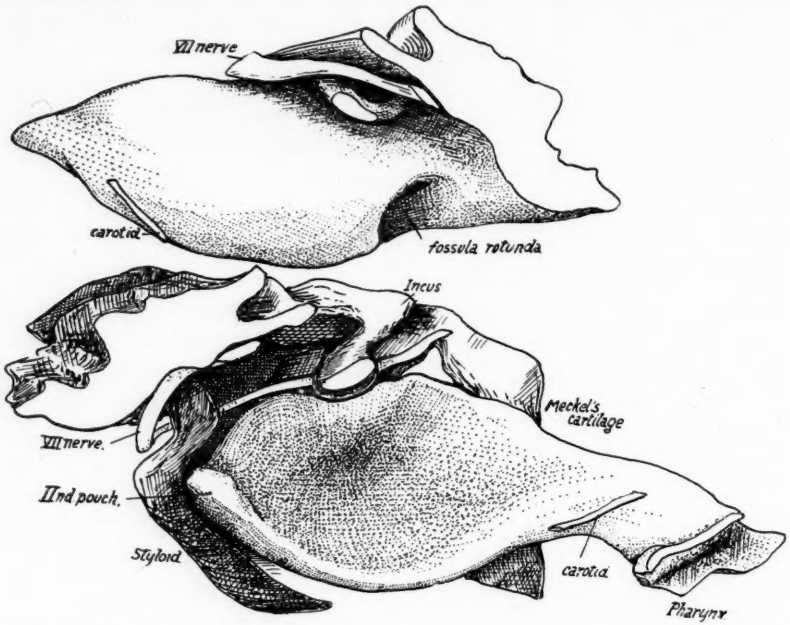

FIG. 6.—From model of left middle ear region in 50-mm. specimen. Somewhat simplified. Lower figure shows superficial view of recess seen from above and behind. Note position of 2nd pouch and its relation to the concavity, visible on the roof, which lodges the auditory capsule. The upper figure shows the cochlear portion of capsule cut away from the rest and turned round to exhibit the fossula rotunda which lies over the pouch. Above this the facial nerve and stapes are seen cut, their other parts remaining on the other portion of the model. The thickness of the walls, of course, makes the pouch appear more prominent than it would be if the region were exposed as in the previous figures.

probably as a secondary extension: on this matter, however, I cannot make any positive statement, and must be content with the account already given—that it corresponds with the fossula rotunda in the later third-month stages. Both the fossula and the sinus are internal to the tympano-hyal, so that one or other—or both—might mark the situation of the remains of the pouch.

The secondary sulci in relation with the outer wall of the tympanum

developed from the floor of the recess may be briefly mentioned here. The posterior recess of Tröltsch has already been noticed forming immediately behind the developing manubrium; it deepens somewhat rapidly, and by the third month shows a tendency to extend up to the outer side of the chorda tympani. In this rate of extension it differs from the sulcus in front of the handle which marks apparently the remnant of the first groove; this is deep in the 16-mm. embryo, and later becomes partly filled up and shallower, so that its presence in the third month appears to owe its evidence as much to the prominences at each side of it as to any inherent depth it may possess. Probably the anterior recess of Tröltsch is secondarily derived from it, but even in the fourth month there is only a very slight increase in the relative depth of the groove. The different powers of extension which are exhibited by the two sulci may have something to do with the fact that the posterior recess is said to communicate with the pouch (Prussak's) above it, but that this never occurs with the anterior recess.

The consideration of the nerve supply of the walls of the tympanic cavity would seem to belong more appropriately to the account of the formation of the roof of the tubo-tympanic recess and its subsequent development, but, as the second arch is represented in the floor or outer wall, one might expect to find an area over which the nerve of the second arch distributes filaments. Such an area is quite unknown—at least, I am not aware of a description of a sensory supply of this sort ever having been given, and I have failed to find any indication of its existence in sections at the fourth month. If such an area did exist, one would expect it to be very small, limited to the mucous membrane over the tympano-hyal, for the remainder of the second arch has been invaded by extension from the first arch, and this has carried its nerves and vessels with it.

The condensation of this manubrial extension is placed between the meatus and the floor of the recess, and is much thicker above than below. The thick upper and outer part can again be divided into an inner part in which the handle is formed, and an outer which is continued into the thinner layers of the lower and inner portion: these two by their subsequent thinning out make the membrane, which is therefore on the outer side of the handle of the malleus. Thus the manubrial mass is not only concerned with the manubrium but also with the membrane, this portion of it being thinned out apparently by the pressure of the meatal plate growing toward the cavity: perhaps the thicker and looser and more vascular tissues of the membrane of Shrapnell may represent the upper and less compressed part of the condensation. The nerves of the condensation are carried backwards and downwards with it. They thus belong to the auriculo-temporal group of the mandibular, and one of them (the superior meatal of auriculo-temporal) runs back over the top of the meatal plate and turns down in the condensation with the handle of the malleus; it lies outside and behind the

handle, running parallel to it, and gives off filaments which pass radially to the whole periphery of the membrane, round which they turn to be distributed to the region of the meatus. I cannot help thinking that these branches are also supplied to the tympanic aspect of the structure. Todd describes connexions between this nerve and the chorda tympani: I have not been able to find these certainly, nor any indication of other nerve supply. It seems to me that a supply from the auriculo-temporal might be expected over the tympanic aspect of the membrane as far up as the chorda, but my observations made with bearing on the question have been very unsatisfactory in their results, and I have been unable to reach definite conclusions on the matter.

While on the subject of nerves related to the tympanum, it is not out of place to call attention to the position of the chorda as seen in the models and figures given in this paper. It is a common—though not perhaps a general—teaching that the facial nerve does not possess a representative of the pretrematic branch of the typical branchial nerve, but that the ninth nerve shows an example of it in its tympanic branch. The conditions as found in the embryo appear to be quite clearly against this view. The chorda passes from the region of the second arch over the first pouch into the first arch, and is thus strictly comparable with a pretrematic branch: although the subsequent secondary evolution of the cavity leaves the nerve along the outer wall, this is owing to its maintenance of its original and fixed pretrematic course. The ninth nerve, on the other hand, has no branch that passes over the second pouch, at any time in the development, to reach the second arch, and the ramus tympanicus is a branch which seems to be confined to the roof of the recess and to have none of the characters of a pretrematic branch.

In endeavouring to present a picture of the conditions ruling in the developing tympanum, I have been constrained to deal with certain matters only indirectly connected with the proper subject of this communication; but at the conclusion of the whole account I would like to call attention to some points in it on which I wish to lay particular stress. These are:—

1. The original position of the second arch and groove in the floor of the tubo-tympanic recess.

2. Its exclusion from the floor of the inner part of the recess as a result of the growing forward of the third arch over it.

3. The persistence of the arch and groove in that part of the recess which subsequently becomes the tympanum. The partial invasion of it here by the structures associated with the membrane, but its existence purely as second arch in the tympano-hyal region.

4. The formation of the narrow tubal region from the wider inner part of the recess by a direct fusion of the masses of the first and third arches as a sequel to the great forward growth of the latter.

5. The position of the second pouch at the fossula rotunda or sinus tympani, or both, and of the first pouch in the situation of the anterior recess of Tröltsch.

INVESTIGATIONS IN THE ANATOMY OF THE PALATE.

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THE present paper has to do with certain points in the musculature and arterial supply of the palate. The illustrations are taken from a series of dissections which were made during an inquiry into the operative treatment of cleft palate. The observations made differ in a number of particulars from the generally accepted views, and are recorded on that account.

In the case of the muscles of the palate, the conditions represented in the figures have been found in a considerable number of dissections, so that they may be regarded as normal; as regards the arteries, however, the statements are made with more reserve, because neither time nor material sufficed for the making of such a large number of dissections as would be necessary before dogmatic assertions could be made.

Fig. 1 shows the region of the sinus of Morgagni of the right side. Attention is called particularly to the tensor and levator palati, and to the Eustachian tube.

The *tensor palati* is easily recognised in any dissection in which it is displayed, from its breadth, and from the large number of tendinous fibres which it contains (see fig. 5). It arises in five situations: (1) from the inner aspect of the spine of the sphenoid, or from the great wing immediately in front of this; (2) from the scaphoid fossa; (3) between these two points, the muscle does not arise from bone, but from the lateral lamina of the cartilage of the Eustachian tube; (4) by its deep aspect, from the membranous part of the tube; (5) from the posterior border of the internal pterygoid plate. The tendon of the muscle, having passed superficial to the upper fibres of the superior pharyngeal constrictor, and turned inwards round the hamular process, at once expands so as to occupy the anterior third of the soft palate; in this manner is formed the *palatal aponeurosis*, which is not a separate structure, but is actually the expanded tendon of the tensor palati. The posterior border of this aponeurosis gives origin to

certain other muscles of the palate, especially the palato-pharyngeus (see fig. 3); while the anterior border is attached partly to the posterior border of the horizontal plate of the palate bone, and partly, passing forward beyond this, to the transverse ridge upon the oral aspect of that bone.

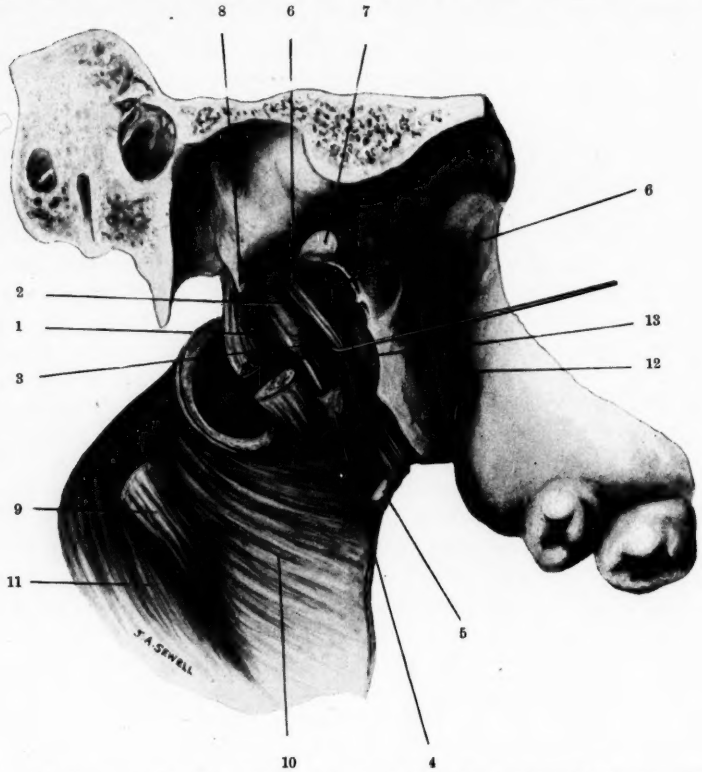

FIG. 1.—A dissection of some of the muscles of the soft palate. The levator palati has been divided, and its proximal half drawn backwards: the posterior border of the tensor palati is seen hooked forwards. A glass rod has been passed along the Eustachian tube, and an opening made into the latter close to its pharyngeal extremity.

1, levator palati; 2, cartilage of Eustachian tube; 3, membranous lamina of Eustachian tube; 4, wall of naso-pharynx at point of entry of tube; 5, hamular process; 6, the bony origins of the tensor palati: between them is seen a part of the cartilage of the tube; 7, foramen ovale; 8, spine of sphenoid; 9, stylo-pharyngeus; 10, superior constrictor; 11, middle constrictor; 12, external; and 13, internal pterygoid plate.

Although the tensor palati undoubtedly acts to some extent as a tensor of the soft palate, yet this action is greatly limited, first by its extensive insertion into bone, and secondly by the fact that its aponeurosis is confined to the anterior third of the soft palate.

The action of the muscle as a dilator of the tube, if such action exist, can only be very slight, owing to the nearly vertical direction of its thin sheet of muscular fibres (see fig. 6). The Eustachian tube is seen in a transverse section as a narrow, vertically placed slit. The outer boundary

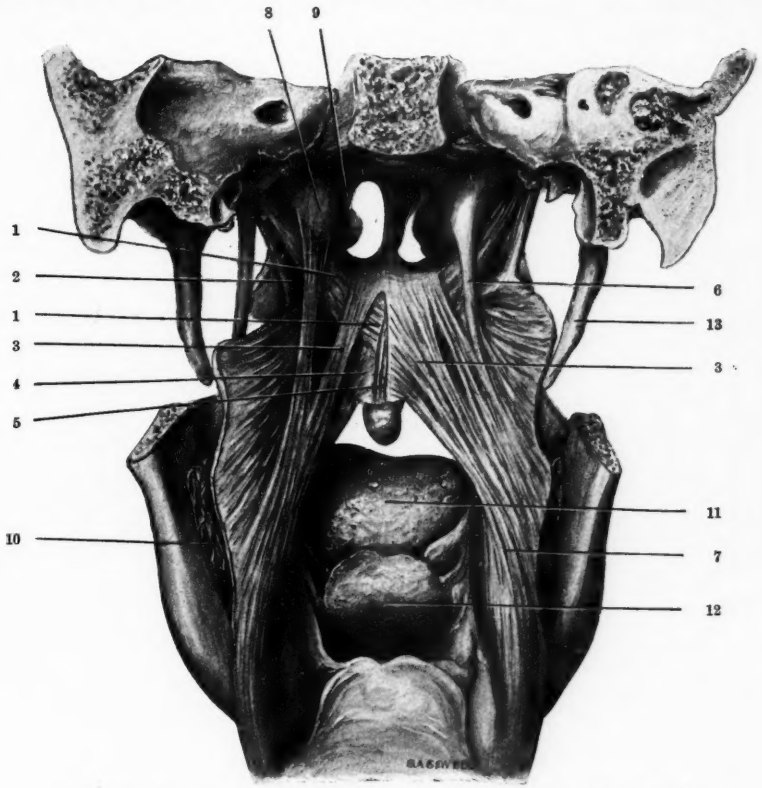

FIG. 2.—A dissection of the muscles of the soft palate and its neighbourhood.

1, 1, levator palati; 2, tensor palati; 3, dorsal part, and 4, ventral part of palato-pharyngeus: on the left side a part of the dorsal division has been removed, in order to show the levator palati, and 5, the azygos uvulæ; 6, salpingo-pharyngeus; 7, insertion of palato-pharyngeus into pharyngeal aponeurosis; 8, Eustachian tube; 9, inferior turbinate; 10, cut edge of mylo-hyoid muscle; 11, tongue; 12, epiglottis; 13, styloid process.

of this slit is formed for the most part by the membranous lamina of the tube, in contact with which, and partly arising from it, is the tensor palati; contraction of this muscle is much more likely to press together the sides of the slit, so as to produce closure, than to bring about opening of the tube.

The anatomy of the *levator palati* is shown in figs. 1, 2, 3, and 6. The thick, rounded belly of the muscle is in marked contrast to the flattened tensor. It has quite a small origin, from a rough area of the petrous bone immediately in front of the inferior aperture of the carotid canal; the quadrate area upon the inferior aspect of the apex of the petrous bone does not give origin to the muscle; nor does the latter arise, by more than a very few insignificant fibres, from the medial lamina of the cartilage of the Eustachian tube. The relation of the muscle to the tube is also worthy

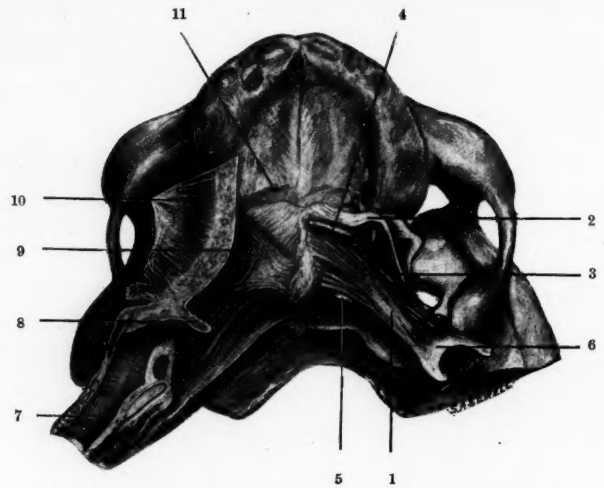

FIG. 3.—A dissection of some of the muscles of the palate of a full-term fœtus. The base of the tongue and the larynx have been split in the middle line, the left half removed, and the right half turned to the right side.

1, levator palati; 2, tendon of tensor palati turning round hamular process: a glass rod has been placed under the tendon; 3, rod in Eustachian tube; 4, 5, the two parts of the palato-pharyngeus, cut short; 6, tympanic bone; 7, trachea; 8, epiglottis; 9, palato-glossus; 10, tongue; 11, suture between palatal processes of maxilla and palate bone.

of note; it lies along, and is closely applied to, the posterior or inferior border of the tube, and rather to the outer side of the latter, not at all upon the inner side, where it is usually described as lying (see fig. 2).

The muscle passes downwards and inwards to the soft palate, above the upper border of the superior constrictor; the upper fibres of the latter muscle here separate the levator and tensor palati from each other. Entering the soft palate immediately in front of the salpingo-pharyngeus muscle, and between the two layers of the palato-pharyngeus, the muscle extends inwards to the middle line, its fibres running as much inwards as downwards. A dissection such as that shown in fig. 2 makes it plain that

this muscle must have nearly, if not quite, as much action as a tensor as as a levator of the palate. Without doubt, it, more than any other muscle, tends by its contractions to separate the sutured edges after the operation for cleft palate, unless it has been divided or in some other way put out of action.

As regards the action of the levator palati upon the Eustachian tube,

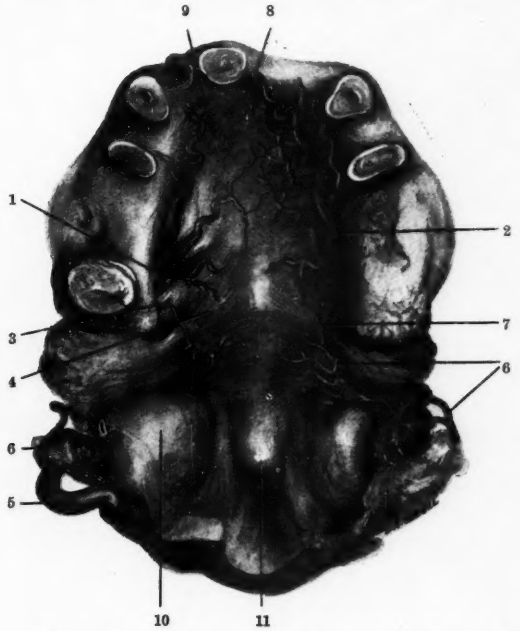

FIG. 4.—A dissection to show the arterial supply of the palate. On the right side the descending palatine artery becomes obliterated before reaching the anterior palatine canal, probably as the result of some inflammatory process connected with the root of a carious right lateral incisor tooth.

1, posterior palatine canal; 2, descending palatine artery; 3, accessory palatine foramen; 4, aponeurosis of tensor palati; 5, facial artery; 6, 6, ascending palatine artery; 7, anastomosis between accessory and ascending palatine arteries; 8, terminal branch of descending palatine artery at anterior palatine canal; 9, old abscess cavity, resulting from carious tooth; 10, tonsil; 11, uvula.

its contraction can exercise no direct pull upon the tube, since none of the fibres of the muscle arise therefrom; but the intimate relation of the muscle belly to the inferior border of the tube suggests other possibilities (see figs. 2 and 6). It has been suggested that the contracting muscle belly might bulge upwards to such an extent as to obliterate by its pressure the lumen of the tube; such an action can scarcely be possible,

even at the pharyngeal orifice of the tube, where under ordinary circumstances the levator palati produces something of a swelling upon the floor; for even here it is difficult to close the lumen of the tube, even by forcibly pushing the muscle upwards towards it. It is much more probable that the muscular contraction opens the tube, in one or both of two ways:

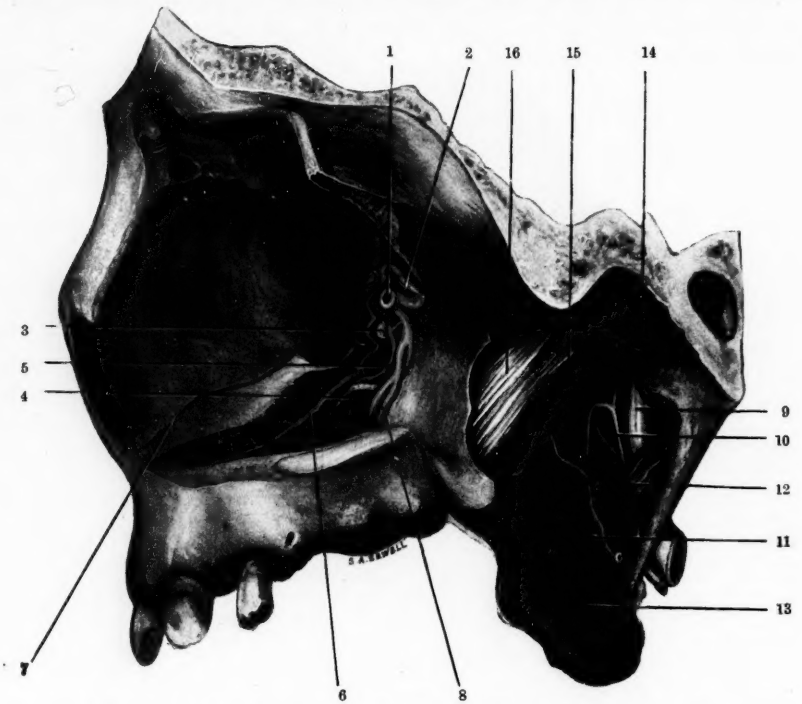

FIG. 5.—A dissection to show the arterial supply of the palate. The bones forming the outer wall of the left nasal fossa have been removed to show the course of the naso-palatine artery.

1, termination of internal maxillary artery; 2, spheno-palatine artery; 3, stump of middle turbinate; 4, stump of inferior turbinate; 5, lateral nasal branch, and 6, naso-palatine branch, of spheno-palatine artery; 7, cut edge of mucous membrane covering septum nasi; 8, descending palatine artery; 9, internal carotid artery; 10, ascending pharyngeal artery; 11, ascending palatine artery; 12, stylo-pharyngeus; 13, superior constrictor; 14, tympanic bone; 15, levator palati; 16, tensor palati.

(1) by pressing upon the inferior border of the tube so as to cause its lumen to open in a transverse direction; (2) by tilting the whole of the cartilaginous part of the tube, so as to bring it more into line with the bony portion.

The *palato-pharyngeus* is shown in figs. 2 and 3. The observations

made agree with the published descriptions, except in two particulars: (1) the posterior lamina arises not only from the middle line of the soft palate, but also, at its most anterior part, from the dorsal aspect of the palatal aponeurosis, immediately in front of the levator palati; (2) the anterior lamina takes origin from the horizontal plate of the palate bone not directly, but by means of the palatal aponeurosis, to the posterior border of which the muscle is attached. It also arises, behind this, from the middle line of the palate.

Figs. 4 and 5 are taken from a dissection showing the arterial supply of the palate.

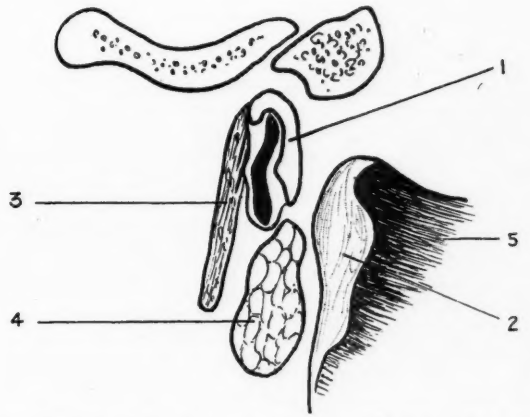

FIG. 6.—From a coronal section of the head, passing through the left cartilaginous Eustachian tube.

1, medial lamina of cartilage of tube; 2, cushion of Eustachian orifice; 3, tensor palati; 4, levator palati; 5, cavity of naso-pharynx.

By far the most important vessel supplying the hard palate is the *descending palatine artery*; it is a large vessel, which traverses the posterior palatine canal, enclosed in a tube of periosteum. Still lying in the periosteum, the artery takes a tortuous course forwards towards the anterior palatine canal, giving branches inwards to the hard palate, and outwards to the alveolar process and to the gum; the branches to the hard palate are tortuous, like the parent stem, and anastomose freely with one another, and less freely with those of the opposite side.

The accessory palatine branches, given off in the posterior palatine canal, pass through the accessory palatine foramina and turn backwards to anastomose with the ascending palatine arteries. The terminal branch of the descending palatine artery turns upwards through the anterior

palatine canal, and, on the nasal septum, anastomoses with the *naso-palatine branch of the spheno-palatine artery.* Should the descending palatine artery be obstructed or divided, this anastomosis would not as a rule bring any large amount of blood to the hard palate, owing to the small size of the naso-palatine artery; the parent trunk of the latter, the spheno-palatine artery, is large as it arises from the internal maxillary, but is much diminished in size by giving off lateral nasal branches to the turbinate bones, so that only a small branch remains to carry blood to the palate.

It becomes of importance, therefore, in operating for cleft of the hard palate, to place the lateral incision (through which is introduced the elevator used to separate the muco-periosteal flap from the bone) as far externally as possible, in order to include the descending palatine artery in the flap, and thus to secure the vitality of the latter. The incision should be directed outwards against the alveolar process, rather than upwards against the palate, as otherwise the artery may suffer injury or its branches be divided.

Just as the descending palatine artery is of chief importance in the supply of the hard palate, the main artery to the soft palate, in the dissection shown, is the *ascending palatine* (branch of the facial). It is seen in figs. 4 and 5, arising from the facial artery, passing upwards superficial to the stylo-pharyngeus and superior constrictor, and then turning inwards above the upper border of the last-named muscle to reach the soft palate along with the levator palati. It is seen to give off the tonsillar artery, which reaches the tonsil by piercing the superior constrictor.

Summary.

1. The palatal aponeurosis is actually the expanded tendon of the tensor palati.

2. The levator palati has only a small origin from the petrous portion of the temporal bone, immediately anterior to the inferior aperture of the carotid canal.

3. The levator palati is the most powerful tensor of the soft palate.

4. Contraction of the tensor palati probably closes the Eustachian tube, while contraction of the levator palati probably opens it.

5. The dissections tend to show that the most important arteries of the palate are, to the soft palate, the ascending palatine branch of the facial; and to the hard palate, the descending palatine branch of the internal maxillary. The naso-palatine artery, as far as the blood supply of the palate is concerned, is small and relatively insignificant.

PARIETAL PERFORATION ACCOMPANIED WITH FLATTENING OF THE SKULL IN AN ANCIENT EGYPTIAN.

By Douglas E. Derry, M.B., Ch.B., *Lecturer in Physical Anthropology, University College, London.*

Although cases of perforation of the parietal bones have been recorded in this Journal and elsewhere on several occasions, the condition is sufficiently rare to justify the publication of the present example, especially as this case differs in certain important particulars from those already described.

The skull, a photograph of which is shown in fig. 1, was found by Mr R. Engelbach at Shurafa, Lower Egypt, in a cemetery of Roman date, which he was excavating for the British School of Archæology, and I am indebted to him for preserving it and bringing it to this country, and to Professor Flinders Petrie for his permission to publish this account.

The skull is in perfect condition, only a few teeth having dropped out since removal from the grave, and from its general characters is probably that of a young woman of about twenty-one years of age. All the cranial sutures are open, and the basilar synchondrosis is becoming ossified. In the mandible the wisdom teeth are fully erupted and level with the rest; and although in the maxilla they appear to be still not perfectly on a level with the other teeth, this is probably due to the natural upward curve of the posterior ends of the alveolar arch, as they are in perfect apposition with the lower third molars when the mandible is articulated. In this connexion it may be noted that the teeth appear to be practically unworn, a condition which, in an Egyptian of this age, is, in my experience, unparalleled. The possible significance of this will be referred to later on.

External Aspect.—Except for the condition now to be described the skull appears to be quite normal. In the *right* parietal bone, close to and involving the sagittal suture, and situated exactly opposite the obelion, or, in other words, near the site of the right parietal foramen, is a large hole, measuring 24 mm. in the diameter parallel to the sagittal suture and 26 mm. at the widest part of the hole, at right angles to the antero-posterior diameter. As may be seen from the photograph (fig. 2), the hole is irregularly circular, and is incomplete at its inner margin where it breaks into the sagittal suture. Its edges are perfectly smooth and bevelled

externally, and about 8 mm. from the margin of the hole there is a faint suggestion of a bony elevation running concentrically round the opening. The bone here and over both parietals, especially near the middle line, is very finely pitted. This pitting is not visible below the temporal lines. Except for these manifestations there are no signs of inflammatory reaction. From the hole downwards as far as the superior angle of the occipital bone, and laterally involving the posterior-superior angles of both parietals, as well as an area adjacent to these angles, the skull is markedly flattened (fig. 1). The depression of the bone, exclusive of the hole itself, is greatest immediately below the opening and exactly over the posterior end of the

FIG. 1.—Profile view, showing flattening in posterior parietal region.

sagittal suture; but below the lambda the flattening has affected the right side of the skull more than the left, so that the left side of the occipital bone seems to bulge when compared with the corresponding part to the right. From this it would appear that there is an association between the perforation of the bone and the flattening.

On the left side the parietal foramen is represented by a minute hole. At the anterior superior angle of the left parietal bone, and passing across the coronal suture on to the frontal, is a shallow oval depression ($19 \times 8{\cdot}5$ mm.) with a roughened floor, perhaps the result of an injury.

Internal Aspect.—All the sutures are open internally. The sulcus for the superior longitudinal sinus, which anteriorly is placed exactly in the middle line over the sagittal suture, is at the site of the perforation deflected to the left, coming again into the middle line after passing the opening in

the parietal bone. The inner margins of the parietal bones at the point where the hole touches the middle line are thin and translucent. There are two depressions on the inner table of the right parietal bone behind the perforation and between it and the lambdoid suture, in one of which the bone is translucent. This depression measures not less than 3 cm. in length and 1 cm. in breadth. It lies vertically, and is deeply excavated in its upper part, but becomes shallow as it approaches the lambdoid suture. These depressions do not affect the outer table. There is a similar elongated depression on the left parietal bone in the same situation, which reaches the left lambdoid suture. The bone here is also translucent. All of these de-

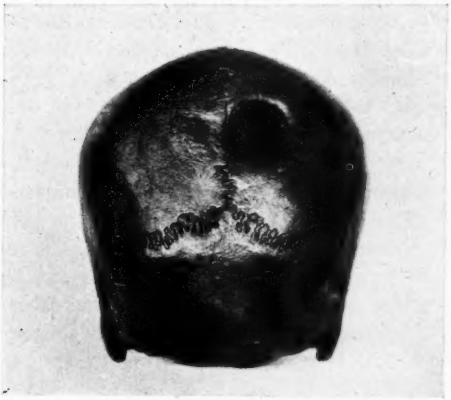

FIG. 2.—Posterior view, showing position and shape of the parietal perforation which just breaks into the sagittal suture.

pressions, as well as the great perforation itself, have large branches of the meningeal vessels running directly to them. The superior longitudinal sinus bifurcates below the lambda, the deeper and better marked of the two channels passing to the left. Just below the point of bifurcation there is a deep depression to the right of the middle line, perhaps associated with the occipital sinus. The *left* side of the occipital bone and the posterior part of the left parietal bone are translucent, but on the right side the density of the bone is greater and no light passes through in the corresponding positions.

It is necessary, before discussing the cause of this opening in the cranial wall, to eliminate the possibility of this being an ancient example of trephining, a practice which was not uncommon in neolithic times in Europe. Sir Victor Horsley, to whom I showed this skull, believed that this might

be a case illustrating an old trephine wound. I had not entertained such a possibility, because the character of the opening is unlike those in neolithic skulls which have been generally attributed to surgical interference, as in the cases described and figured by M. Manouvrier (1). There is, however, some resemblance to the present instance in a case published by Manouvrier (*op. cit.*), which differs from others recorded by him in the absence of any signs of inflammatory reaction at the edges of the opening. There is also considerable thinning of the bone in the neighbourhood of the hole, which Manouvrier believes to have been caused by the removal of the periosteum by the prehistoric surgeon, or by some accident, for which subsequently the operation was performed.

An examination of old trephine wounds from cases operated upon at the National Hospital, which Dr F. E. Batten very kindly allowed me to see, shows that while extensive healing of the cut edges of the bone takes place, there is nothing in the nature of bevelling to be seen, while traces of the original inflammation are very obvious.

But from the Egyptian skull itself we can obtain the most important evidence against trephining; for the superior longitudinal sinus is, as already described, deflected to the left on reaching the opening in the right parietal bone. It skirts the margin of the hole, lying altogether, at this point, upon the left parietal, and only returns to the median line after passing the opening. Now, the position of the sinus is remarkably regular under normal circumstances. It does not slavishly follow the course of the sagittal suture, should the latter deviate from the middle line, as may be seen, for example, in a hydrocephalic skull preserved in the Anatomy Museum at University College, where the groove for the longitudinal sinus is absolutely central, while the sagittal suture takes a course obliquely across it. Such a displacement of the sinus groove as exists in the Egyptian skull can only have been brought about in early life, and must mean a pushing of the falx and with it the contained sinus to one side by something which occupied the site of this large foramen and encroached upon the middle line. Had this opening been made artificially, such a displacement would have been impossible, and it is more than likely that the sinus itself would have been opened, with probably fatal results, as in its normal median position it would have been well within the circumference of the opening. Further, the theory of trephining does not explain the flattening, unless, as Sir Victor Horsley suggests, the operation was performed on account of the deformity, which, to say the least of it, appears to me most improbable—if not, in the light of what has been said in regard to the position of the sinus, impossible. Lastly, no case of trephining has so far been recorded in any Egyptian skull, though probably more crania of this

race have been examined and carefully studied than of any other people either ancient or modern.

The first case of a skull exhibiting perforation of the bones was described by Turner in 1865 (2). The skull-cap belonged to a woman aged twenty-five, who had been operated upon for the removal of a cyst of the scalp which had been present all her life, but had recently commenced to increase in size. Death took place from meningeal sepsis, and at the subsequent post-mortem examination it was found that there was an opening in the middle line of the occipital bone at the site of the cyst. There were also two further openings, one in the posterior part of each parietal bone, in the neighbourhood of the normal parietal foramina. The sagittal suture between these openings was obliterated, and the superior longitudinal sinus was deflected between the two apertures, to the right. All of the openings were closed by cribriform fibrous membranes. Turner considered the parietal openings to be exaggerated parietal foramina.

In the following year Wrany (3) described four skulls with large parietal foramina, but in only one of these were the openings of a large size, measuring respectively three-fifths and four-fifths of an inch in diameter. He believed that the large size of the opening was associated with an enlarged condition of the perforating branches of the meningeal arteries, and compared his cases with Turner's.

In 1870 Grüber (4) described two cases of the same enlarged condition of the parietal foramina, and again in 1876 (4) he published a further case of this anomaly and discussed possible causes. He appears to conclude that there is no relation between the production of the foramina and the meningeal vessels. The holes are due to a lack of ossification of the bone at this site, but the reason of such failure is obscure.

In 1892 Greig (5) published an interesting case of congenital and symmetrical perforation of both parietal bones in a soldier, then living. The openings were large, the right measuring $3{\cdot}6 \times 2{\cdot}7$ cm., the left $2{\cdot}5 \times 2{\cdot}3$ cm. Between the two unossified areas there was a narrow bridge of bone about 2 cm. wide in the course of the sagittal suture.

In 1895 Symmers (6) recorded a case of "enormous parietal foramina" in the skull of a man aged forty who died of acute pneumonia. In each parietal bone there was a large hole, the left 21×14 mm., with smooth rounded and distinctly bevelled margin; while the opening in the right bone presented the same characters but was smaller, 15×14 mm. "During life the dura mater was adherent through the foramina to the pericranium, forming a tough fibrous membrane, which effectually closed the openings." . . . "The father of this man had a similar abnormality."

In 1900 Paterson (7) published three cases of symmetrical perforations

of the parietal bones, accompanied by excellent plates, which illustrate very clearly the position of the apertures and their relation to the normal parietal foramina. In some of the fœtuses which he examined similar deficiencies were present, but not in the exact situation of the parietal foramen. Paterson is inclined to associate these perforations with inequality of growth in the cranium and cerebrum, by which the latter has exerted pressure upon the ossifying bone and thus retarded its formation, and in support of this he draws attention to the microcephalic character of the cranium recorded in some of the cases, and believes that, in the case he describes, arrest of development of the base of the skull and closure of sutures may account for the existence of these great perforations.

Paterson's theory receives further support from a case published by Paul-Boncour (8). The skull-cap examined had belonged to an idiot, who was also blind and suffered from epileptic fits. Death took place at the age of thirty-three. There was complete synostosis of the skull, which was trigonocephalic owing to congenital closure of the metopic suture, and acrocephalic from the same early synostosis of both the coronal and sagittal sutures. There were symmetrical perforations at the site of the normal parietal foramina, measuring 13 mm. transversely and 5 mm. in the antero-posterior diameter.

Although, in the cases described by the observers just quoted, there are great differences in the size of the perforations and also in the accompanying conditions, they all agree in regard to the position of the apertures, which are invariably situated at or about the site of the normal parietal foramina—that is, close to the obelion; and this part of the sagittal suture is generally synostosed in association with such perforations, whatever the condition of the rest of that suture. It is generally recognised that the parietal foramina are the remains of the two clefts, one in the upper border of each parietal bone near its posterior end, which are normally present during ossification of the bone. These clefts, together with the intervening space in the line of the sagittal suture, form the sagittal fontanelle, which is usually closed before birth. At this point, according to Paul-Boncour (9), ossification takes place more slowly, and there is thus, in this part of the cranial wall, a predisposition towards perforation which may be taken advantage of by vascular, meningeal, or cerebral anomalies. That these perforations do occupy the site of the original fœtal clefts is borne out by their symmetry, the constancy of their position, and also by the fact that the long axis of the aperture is in almost every case transversely placed.

Although in some of the cases, Paterson's, Paul-Boncour's, and one of Wrany's, in which the child of three years and two months died of tubercular disease and hydrocephalus, there was deformity of the skull accompanying

the perforations, this is by no means always so, for some of the best-marked instances are perfectly normal in cranial form.

Again, the somewhat natural assumption that such large apertures must have been produced by something protruding through the skull wall finds no support from those cases which have been seen with the soft parts *in situ*. Neither in Greig's case, in which the apertures had been recognised since childhood, nor in that reported by Symmers was there any sign of a cause for the perforations. But in Turner's case, although nothing apparently existed to explain the symmetrical parietal openings, there was a dermoid cyst definitely related to the hole in the occipital bone, which measured 2·5 cm. in vertical direction and 1·25 cm. transversely. It is difficult to believe that the presence of the parietal perforations in the same skull was merely a coincidence, and that in early life there had not been some similar cause at work which might account for these deficiencies. That dermoid cysts do cause lack of ossification in the underlying bone is well known. Mr Shattock has very kindly given me particulars of such a case in the museum at St Thomas's Hospital, in which in the skull of a child of eight months there is a membranous area in the middle line of the frontal bone immediately beneath a dermoid cyst. I know of another case in which a dermoid cyst was removed from the neighbourhood of the external angular process of the frontal bone. Here again an unossified area in the cranial wall was discovered by the surgeon, which prevented the complete removal of the cyst owing to its attachment to the subjacent membrane.

The question now is whether such a condition could satisfactorily explain the large hole in the Egyptian skull. It has been shown that large perforations may be present without any apparent cause, and we might consider the present case to be one of these. There are, however, two facts which differentiate the condition in this skull from all of the others recorded with which it may reasonably be compared. In the first place, the opening is unilateral. Now, in none of the crania with *large* parietal perforations is this the case. In three of Wrany's cases and two of Grüber's the perforations were quite small, evidently merely enlargements of the normal foramina, and in one or two of these only the foramen of one side was affected; but in all of the cases in which the openings are of large size they are symmetrically placed, one on either side of the sagittal suture, and there is generally a well-marked bar of bone between the two holes. In one of Paterson's cases the intervening bar is incomplete and the two apertures are thus united. Here, too, the longitudinal sinus deviated from the middle line and appeared to end in front of the left aperture.

The second point of difference in the Egyptian skull is the flattening

below the aperture. It is difficult to avoid the conclusion that the parietal perforation and the accompanying deformity of the skull are causally related. When I first saw this skull I was inclined to the belief that a hernia of some sort must have been responsible for the opening and for the flattening below it. But cerebral meningocele, which seemed the most likely explanation, is, I believe, unknown in this situation.

There is, however, still a further condition exhibited by this skull which may bear strongly on the argument. It has already been said that the teeth are scarcely worn. For an Egyptian skull this is remarkable in a girl of at least twenty years of age. Two other skulls from the same cemetery and of similar age, *i.e.* below twenty-five years, both with excellent teeth, show nevertheless considerable wear, particularly, of course, of the first molars, which have been longest in use. This is not the case with the teeth of the perforated skull. The first molar is the only tooth which shows marked signs of wear, and these are comparatively small, consisting of slight facetting of the cusps where the opposing tooth has met them. The incisors are also slightly chiselled, as well as the canines, but the general appearance of the teeth suggests that the amount of mastication performed by the jaws was unusually small. But this is not all. The enamel of all the teeth, with the exception of the lower incisors (the upper central incisors have dropped out recently), is pitted and irregularly laid down (fig. 3). It is interesting to notice that the first molars are the least affected. Now, it is well known that interference with nutrition in early life, when the teeth are calcifying, tends to affect the structure of the teeth, and such interference produces the condition known as hypoplasia of the enamel. Mr Sidney Spokes (10), to whom I showed the teeth, considers that this is an instance of such a condition, though of an unusual form. From the fact that the first molar, which has commenced to calcify at birth, shows signs of this change, although to a slighter degree than the others, it is inferred that the factors responsible for this affection of the enamel had already commenced to operate even at this early date, and became progressively more effectual as time went on, for the third molars exhibit this change more clearly than any of the other teeth. Finally the lower incisors are thickly covered on the labial aspect with tartar, a condition which Mr Spokes considers was probably associated with mouth-breathing and a depressed lower lip. In this connexion it should be mentioned that the left middle turbinate bone is much swollen and reaches the middle line, pushing the septum to the right. Close to the anterior attachment of the turbinal is an opening into the left antrum.

Now, if we sum up all the evidence yielded by this skull, it seems clear that the unilateral character of the perforation in the parietal bone,

accompanied by the deformity of the skull in the neighbourhood of that perforation, and more particularly on the same side as that upon which the hole is situated, differentiates this case from those quoted above in which the holes are always symmetrical and in which associated flattening of the bone is absent. At the same time, this very flattening, as well as the alteration in position of the sinus, points to the existence of the conditions responsible for these peculiarities, at a very early period of life, and this is further borne out by the changes in the enamel of the teeth, changes which could only have taken place while the enamel was being laid down, from the time of birth onwards. It is clear, therefore, that this hole in the

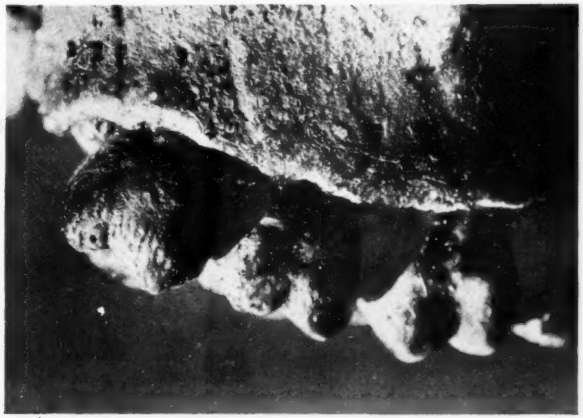

FIG. 3.—The right upper molar teeth of the perforated skull to show the condition of the enamel, particularly in the wisdom tooth.

parietal bone must be either of congenital origin or have been produced within the first few months after birth; and if it is, as I believe, related to the flattening, it seems necessary to suppose that something protruded from this aperture and depended in such a way as to flatten the bones upon which it lay, immediately beneath the foramen.

Cases of traumatic encephalhydrocele in children are well recognised. The injury to the cranial wall generally takes the form of an elongated slit, which enlarges very rapidly, and the edges are everted. Dr F. E. Batten very kindly showed me such a case, over four years after the accident, which was due to the baby being dropped and striking its head on a sharp projection. The wound in the skull is at the present time 10 cm. in length, and stretches right across the right parietal bone from

the lambdoid suture towards the bregma. It was noted at the time of the accident that the injury did not involve the anterior fontanelle, and that it measured 4 inches in length, so that this diameter has not changed. The widest part of the aperture is at the posterior end of the parietal bone, and here pulsation is plainly visible. The edges of the wound are now thickened and rounded off. The mental condition of the child appears to be perfectly normal. In another case, for which I am also indebted to Dr Batten, a similar accident had occurred at about five months of age. The patient, who is now twenty-eight years old, is slightly hemiplegic, but is otherwise quite normal. At the age of nine, when she first came under Dr Batten's notice, there was marked visible pulsation over the wound, which is situated about the centre of the right parietal bone. To a large extent this has become covered in by new bone, and only a small area remains unossified. Here, again, the original injury was evidently of the nature of a split in the bone spreading from the site of the actual blow. In neither of these cases is there the least resemblance to the case under discussion either in position or in the form of the aperture. We may therefore exclude the possibility of injury, and are compelled to recognise that this large opening is congenital, but that its cause remains obscure.

It is, however, possible that such a cyst as that which caused the large opening in Turner's case was also responsible for this; and when all the facts of the present case, so far as we can ascertain them from an examination of the evidence afforded by this ancient skull, are read in the light of the following case described by Dr John W. Ogle (11), it seems not only possible but probable that the Egyptian girl suffered in a similar way and from the same cause.

Dr Ogle's case was that of a boy aged two and a half years, who had not been well for six months, and about twelve days before admission to the hospital had fallen from a chair. The next day it was observed that he squinted, and there was rolling of the eyes and some convulsive movements of the arms, while the neck was tetanically drawn to the left side. There was no insensibility or paralysis. General convulsions of the limbs and body came on before death. At the subsequent examination a cyst, which was contained in the dura mater lining the occiput, was discovered, which had projected into the brain. The cyst was 1½ inches in length and 1 inch in breadth, and corresponded to a depression in the occipital bone, which was very shallow at the lower part but deep in its upper portion, with abrupt margins. Its direction was vertical, and the lower part of the groove for the superior longitudinal sinus was considerably deflected to the left of the median line. The bone forming the hollow was remarkably thin, and at its upper part was pierced by a foramen which admitted a

probe. It opened on the outer surface of the skull, having an oblique upward direction and being bevelled off at the upper margin. Except for this there was no want of union of the bony parts of the occiput. The cyst was formed in the dura nearest the bone and posterior to the sinuses terminating at the torcular. By means of the cyst the lower part of the superior longitudinal sinus and the torcular were pushed much to the left side. The termination of the right lateral sinus was also greatly pushed forwards. The cyst contained hair and sebaceous material, and a few of the hairs passed through the cyst wall to the foramen referred to above.

Now, allowing for differences of position, the conditions described on the inner surface of the occipital bone in the above case are very closely paralleled by the depressions described in the Egyptian skull on the inner surface of the parietal bones, and especially on the right side. Here we have the same thinning of the bone, in association with the depression, which is also, as in Dr Ogle's case, deep in its upper part and shallow below. The deviation of the sinus to which he twice refers has been emphasised in the Egyptian, although in the latter it is related to the aperture in the parietal bone, which is absent in Dr Ogle's case. By way of illustration, Dr Ogle showed at the same time a cyst projecting out into the scalp and obviously connected with intracranial structures.

There can be little doubt that such superficial dermoid cysts may be associated with similar cysts within the skull, and if this is granted, the conditions existing in the Egyptian skull admit of a reasonable explanation. In this case it may be supposed that a large cyst occupied the site of the aperture in the parietal bone, pushing the superior longitudinal sinus to the left, and that it was connected with smaller cysts within the skull which were the cause of the depressions in the cranial wall. The constant pressure of the cyst may account for the flattening of the bone below the aperture. In the light of Dr Ogle's case we may be permitted to suggest that this Egyptian girl from an early age suffered from the effects of cerebral pressure owing to the presence of the constantly growing cysts, and was thus mentally defective, a suggestion which receives support from the fact that the teeth have been scarcely used in mastication, and that they also exhibit definite traces of early and long-standing interference with nutrition. The girl died at about twenty-one years of age, at which time these cysts tend to enlarge more rapidly.

It is not suggested that all cases of parietal perforation are due to cysts, but the association of such perforations with another in the same skull directly due to a dermoid, as in Turner's case quoted above, is very significant, and may possibly explain their presence. It is noteworthy that in this same case Turner describes the superior longitudinal sinus as

being deflected between the two parietal apertures, although there was at the time of death no apparent cause for the anatomical conditions.

I am greatly indebted to Mr Shattock for originally suggesting the possibility of dermoid cyst in this case; and to Dr F. E. Batten for the opportunity of seeing the two cases of traumatic perforation of the parietal bone which I have referred to in the paper. I also owe my thanks to Sir Victor Horsley, Mr Sidney Spokes, and Mr Percy Sargent, all of whom very kindly examined the skull and gave me their opinions upon it.

A list of measurements of the skull is appended to this paper.

Measurements of Skull with Large Parietal Perforation.

Glab.-occip. length	170 mm.	Palate length	45·5 mm.
Ophryo-occip. „	169·5 „	„ breadth	36·5 „
Maximum breadth	131·5 „	Nose height	49·5 „
Frontal „	89·0 „	„ width	23·0 „
Basi. breg. height	131·5 „	Longitudinal arc	349·0 „
Auricular „	117·0 „	Frontal „	111·0 „
Bizygomatic breadth	114·0 „	Parietal „	134·5 „
Bimalar „	95·5 „	Occipital „	103·5 „
Upper facial height	64·0 „	Transverse „	290·0 „
Total „ „	107·5 „	„ „ R.	145·5 „
Basi-nasal length	95·0 „	„ „ L.	144·5 „
Basi-alveolar „	95·0 „	Circumference	487·0 „
Profile angle	80·5°	Foramen magnum, L.	37·0 „
Orbital width, R.	37·5 mm.	„ „ B.	32·5 „
„ „ L.	38·0 „	Capacity (cranial)—	
„ height, R.	33·0 „	by mustard seed	1250 c.c.
„ „ L.	33·0 „	by Pearson's formula	1277·8 „
Interorbital (interdacryal)	18·5 „		

Mandible.

Bicondylar breadth	106·5 mm.	Breadth of ramus (max.), L.	41·0 mm.
Bigonial „	87·5 „	„ „ (min.), R.	31·0 „
Height of symphysis	29·5 „	„ „ „ L.	33·0 „
„ ramus, R.	56·0 „	Mandibular angle, R.	122·5°
„ „ L.	54·5 „	„ „ L.	118·5°
Breadth of ramus (max.), R.	40·0 „		

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A NEW MYLOMETER.

By Douglas E. Derry, M.B., *Lecturer in Physical Anthropology, University College, London.*

In the Report of the Commission appointed by the Thirteenth International Congress of Prehistoric Anthropology and Archæology for the Unification of Craniometric and Cephalometric Measurements, translated by Dr W. L. H. Duckworth (Cambridge University Press, 1913), the following directions are given for measuring the length of the ascending ramus of the mandible (page 13):—

"Anatomical Landmarks:—

"1. Above: superior border of the condyle.

"2. Below: the *gonion*: but since this point is often very difficult to determine, it is recommended to take the point of intersection of the lines representing the lower and posterior surfaces respectively, prolonged till they cut each other. The measurement may be made conveniently by placing the mandible on a plane surface, and placing the bar of the callipers in contact with the posterior border of the ascending ramus."

In actual practice it was found impossible to take the measurement with the callipers as described, accurately.

For this reason the instrument illustrated was devised in consultation with Professor Thane, who suggested the employment of a millimetre scale with a sliding arm, which was to be fixed on a hinged board similar to Broca's mandibular goniometer. This was made experimentally, and proved quite satisfactory. The addition of the protractor attached to the upright board at the back, for measuring the mandibular angle, we owe to Professor Karl Pearson, who by a coincidence was engaged at the same time in constructing a mandibular goniometer.

As both sides of a mandible are seldom if ever symmetrical, it is necessary to measure each ramus independently. For this purpose both the fixed and the movable boards are provided with millimetre scales. In the illustration the mandible is in position for the measurement of the length of the *left* ramus. The line representing the lower border of the body of the jaw is given by the surface upon which the mandible is resting, and this meets the line corresponding to the surface of the hinged board, with which the posterior border of the ramus is in contact, exactly at the centre of the hinge, which at this point is cut down level with the surface of the board, to accommodate the angle of the bone. A T-square sliding

against the edge of the board is brought down upon the condyle, and the length of the ramus from "the point of intersection of the lines representing the lower and posterior surfaces respectively," to the top of the condyle, can be accurately read off. The mandibular angle is read on the protractor without moving the bone. To measure the *right* side, the bone is turned over and made to rest with its right ramus on the fixed board and its body on the hinged board, the latter being readjusted as necessary. We owe the idea of the second scale for measuring the right side also to Professor Karl Pearson.

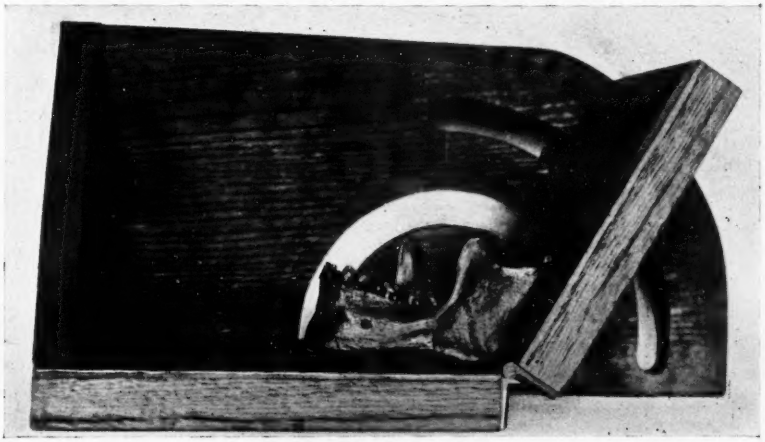

FIG. 1.—Mylometer, with mandible in position, for measuring the length of the *left* ramus, and the angle which it forms with the body of the bone.

Some difficulty was experienced at first in fixing the movable board in the required position during the taking of the measurements. This was solved in a simple and efficient way by the introduction of a clamping-nut, which is attached to the movable board and passes to the back through a slot in the upright board. Thus while the left hand holds the bone in position, the right holding the clamping-nut brings the hinged board into exact contact with the posterior border of the ramus, and by a turn of the screw fixes it in that position. This device is due to the laboratory assistant, G. J. Hancock, who also made the instrument.

Lastly, the eminently suitable name of mylometer, which we have applied to this instrument, was suggested by Professor Thane, whose ideas, coupled with those of Professor Karl Pearson, are responsible for its success.

THE GENESIS OF JACKSON'S MEMBRANE: NOTES ON THE GENITO-MESENTERIC FOLD OF PERITONEUM AND THE SUPRA-ADHESION FORAMEN.

By DOUGLAS G. REID, M.B., Ch.B. Edin., M.A. Trin. Coll. Camb., *Anatomical Department, University of Cambridge.*

(*a*) JACKSON'S MEMBRANE.

WHILST supervising the dissection of an adult I observed a strong membrane (see fig. 1) lying in front of the ascending colon. The cæcum lay in its normal position and was free from adhesions except at the upper part of its posterior wall, where it was fixed to the parietal peritoneum of the iliac fossa. Here it covered the short appendix (3·5 cm. long), which was almost completely buried in the adhesions. The terminal portion of the ileum was also "free."[1]

The transverse colon, in the first part of its course, was bound directly to the ascending colon, in the last 5 cm. of its course, by the great omentum as it passed to the right lateral abdominal wall to form a "right colic ligament."

The connexion was rendered still more secure by adhesions binding the transverse colon directly to the anterior surface of this part of the ascending colon. In this way a permanently acute kink of the bowel was produced at the hepatic flexure. Immediately below this adhesion the transverse colon became horizontal in direction; and so closely were the two portions of the colon bound together that at first there appeared to be an abnormal cæcum-like outgrowth of the bowel.[2]

Crossing in front of the ascending colon and covering the whole of its anterior surface, with the exception of the part which was bound to the transverse colon, was a strong opaque membrane, coated by endothelium. It contained a considerable amount of fat, distributed uniformly throughout, and many blood-vessels, which coursed parallel to one another and at

[1] Apart from its mesentery the terminal part of the ileum may be connected to the abdominal wall by (1) the genito-mesenteric fold of peritoneum; (2) the bloodless fold of Treves; (3) adhesions which bind the ileum directly to the parietal peritoneum (in 50 per cent. of adults).

[2] For skiagrams showing conditions resembling this, see Pilcher's paper, "Surgical Aspects of Membranous Pericolitis," *Annals of Surgery*, January 1912, vol. lv. p. 1.

right angles to the long axis of the bowel. They were visible macroscopically; and the arteries, ultimate branches of the right colic and ileo-colic vessels, crossed the bowel to reach the lateral parietal peritoneum. They gave rise to a transversely striated appearance, seen to some extent in the photograph (see fig. 1). The membrane completely obscured the anterior tænia coli of the ascending colon.

It passed directly from the colon to the lateral abdominal wall without giving rise to any peritoneal fold. Below it faded away upon the cæcum.

FIG. 1.—Case I. Jackson's membrane in an adult, ♂. A knife has been passed between the membrane and the ascending colon, and its blade rests upon the cæcum (also indicated by a hook). A hook has been stuck into the terminal part of the ileum, and another holds forwards the upper part of the membrane which was dissected up from the bowel.

Here it formed a number of strands passing downwards and to the right from the ileo-cæcal junction. It did not pass from the cæcum to the parietal peritoneum, and did not end below in a free edge.

It was a Jackson's membrane.

Above it was continuous with the right colic ligament. It did not bound a pre-colic fossa such as I have described (*Journal of Anatomy and Physiology*, vol. xlvi. p. 401); but the handle of a knife could easily be passed between the membrane and the connective element of the peritoneal coat of the bowel.

As pointed out by Eastman (*Surgery, Gynecology, and Obstetrics*, April 1913), "this would hardly be the case were it a product of membranous pericolitis alone, as suggested by Jackson, or of mechanical irritation alone, as indicated by Martin."

Jackson also draws special attention to its "apparently distinctly detachable nature."

This is illustrated by the fact that before I secured the photograph the dissectors, who were unconscious of the existence of the membrane, had dissected a part of it up from the bowel (see fig. 1).

The ascending colon was not kinked in any way, but was constricted to a remarkable degree, and flattened from before backwards. At its narrowest part it measured 32 mm. from border to border. Above it expanded quite abruptly; and the part which was bound to the transverse colon, as well as the transverse colon itself, had a width of 5 cm.

Traced downwards, the colon, after retaining a uniform diameter for some distance, gradually widened, and the cæcum was 7 cm. broad.

The colic constriction was obviously due to the membrane.

Pieces of bowel between two tæniæ coli were examined microscopically.

The muscular coat of the cæcum was normal in thickness, and all its coats were healthy. The longitudinal and circular layers of the muscular coat[1] of the ascending colon were both much thicker than usual, and on an average were four times as thick as those of the transverse colon.

The connective tissue of the membrane did not "seem to penetrate in increased amount between the muscle bundles" (Hall).

The walls of some of the arteries in the submucous coat were rather thicker, and some of the veins rather larger than normal.[2]

It will be seen that my description differs in some points from that of a membrane given by Hall in Jackson's article, "Membranous Pericolitis" (*Surgery, Gynecology, and Obstetrics*, September 1909).

The fact remains that a sheet was present such as Jackson was the first to point out might become of considerable clinical interest.

It is noteworthy that there was an acute kink of the bowel at the hepatic flexure; and the cæcum lay in its normal position and was neither hypertrophied nor dilated.[3]

[1] It is a mistake to think, as some still seem to do, that in man there is no longitudinal muscular layer between the tæniæ coli.

[2] The body was that of a man aged (?) who died partly as the result of a compound fracture got whilst in a state of alcoholic intoxication.

[3] Compare this with some of the remarks made by Gray and Anderson, University Press, Aberdeen, 1912. It is noteworthy that in none of the adults in which I found a well-marked Jackson's membrane was there "prolapse" of the cæcum such as some say is common; and in none were there angulations of the ascending colon such as are sometimes

The Genesis of Jackson's Membrane.

If we include Case II. (see fig. 2), a well-marked membrane was present in front of the ascending colon in three out of six adults (50 per cent.) whose abdomens were dissected at Cambridge this term (Lent, 1914). In two out of twenty fœtuses I found the parieto-colic fold of Jonnesco formed by a large appendix epiploica. In one it arose from the front of the ascending colon; in the other it crossed in front of the bowel, bounded a pre-colic fossa, and contained arteries, visible macroscopically, which crossed

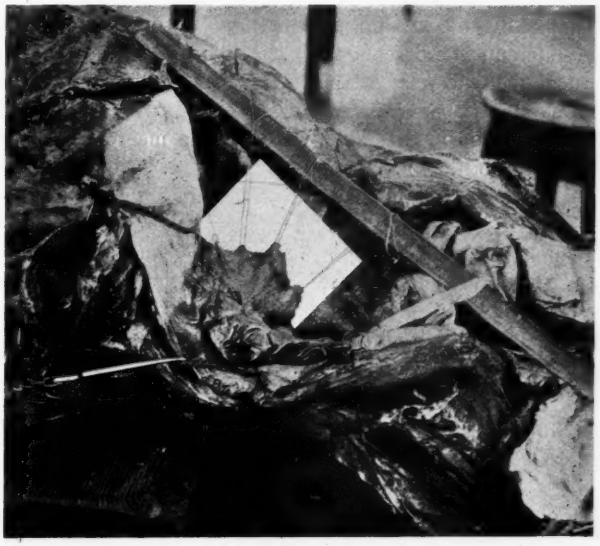

FIG. 2.—Case II. Adult male. The fold of peritoneum referred to has been lifted up from the colon. The upper and lower parts of this appendix epiploica are not shown. It really extends downwards as far as the knife.

the colon, at right angles to its long axis, to reach the lateral parietal peritoneum. A Jackson's membrane is really nothing but a parieto-colic fold of Jonnesco in cases in which this forms an investment for a definite part of the ascending colon.[1]

found in association with the membrane (Jackson). "Recently I have operated on a great many cases of dilated and prolapsed cæca associated with a Jackson's membrane" (H. J. Stiles, personal communication).

[1] Eastman first drew attention to my pre-colic folds in relation to Jackson's "membranous pericolitis" about which I was ignorant at the time my papers were published.

In another adult male I found a fold of peritoneum (see fig. 2), 12 cm. long, and attaining a height of 3·8 cm., lying in front of the ascending colon. Its posterior surface and right border were quite free from any union with the bowel. It contained fat, distributed uniformly throughout, and blood-vessels. It was a large appendix epiploica. It extended from a point just above and internal to the ileo-cæcal junction upwards to the hepatic flexure, and had no connexion whatsoever with the right colic ligament. Below, it arose from the parietal peritoneum (formerly ascending mesocolon) immediately to the left of the colon. Above, it was attached for a distance of 5 cm. to the colon to the left of the anterior tænia coli. Just before passing on to the colon it gained some attachment to the duodenum, which in the descending part of its course was closely bound, as is not uncommon, to the left side of the ascending colon. It covered a number of smaller appendices epiploicæ.

The blood-vessels in this fold were visible macroscopically and lay parallel to one another and at right angles to the long axis of the bowel. The arteries were ultimate branches of right colic and ileo-colic vessels.

I have no doubt as to how the Jackson's membrane in Case I. (see fig. 1) arose. Had the fold in Case II. become fused down to the bowel (and apparently this had occurred to a slight extent over the upper and inner part of the ascending colon), and adherent at its free border to the parietal peritoneum, as in the two fœtuses referred to, a membrane, similar in every respect, would have been produced;[1] and the smaller appendices epiploicæ buried beneath it would have given rise to special "spots and tags of fat" (Hall).

I am not inclined to lay any stress upon the continuity of the membrane in Case I. with the right colic ligament.

In the fœtus the great omentum may adhere to the ascending colon and cæcum (completely descended), and may pass from these to the parietal peritoneum, coating the right surface of the genito-mesenteric fold, and carrying on to it blood and lymph-vessels (*Journal of Anatomy and Physiology*, January 1911).

In two adults I have seen a quite extensive pre-colic membrane formed by the laminæ of the great omentum which had fused together (as may

[1] Although the main blood-vessels in these appendices epiploicæ lay at right angles to the long axis of the bowel, it is possible, should an appendix epiploica adhere to the abdominal wall before the cæcum had completed its descent, that the blood-vessels in it might become oblique. They might then extend from "the inner lower portion of the gut" to its "outer upper peritoneal attachment" (Hall). In cases where the membrane is formed by the great omentum, the blood-vessels in it tend to take a distinctly descending course.

occur extensively in fœtuses from five to nine months old) and become adherent to the ascending colon from which they passed to the right lateral abdominal wall. In both the cæcum was in its normal position. In one the right part of the transverse colon was closely bound to the upper part of the ascending colon simply by this membrane.[1]

In several adults I have noted bands of variable width lying across the front of the ascending colon. These, doubtless, were formed by appendices epiploicæ which had become adherent to the bowel and to the parietal peritoneum.[2]

(*b*) The Genito-Mesenteric Fold of Peritoneum.

This fold was present in seven out of ten (70 per cent. of) full-time fœtuses recently examined by me.

It must be fairly common in children.[3]

In fœtus No. I. (a full-time male) there was a very interesting fold (see figs. 3 and 4).[4] Its mesenteric border (3 cm. long) was related, as normally, to the ileac branch of the ileo-colic artery. Its posterior (parietal) border descended, for a distance of 3 cm., upon the right spermatic vessels. At a

[1] Jackson (*Surgery, Gynecology, and Obstetrics*, 1909) notes that "in some instances it appears as though the membrane came on to the colon from the lateral parietal wall just above the cæcum, and courses directly upwards to disappear beneath the liver on the superior layer of the transverse mesocolon." The transverse colon may also be "drawn down" to the ascending colon by the "membrane."

[2] In some cases a membrane which invests the cæcum, appendix, or indeed the ascending colon, may be formed in other ways. Should the bloodless fold of Treves adhere to the abdominal wall, or should some other adhesion be formed between the bowel and the parietal peritoneum, it is possible that during cæcal descent and torsion, the bowel may gain an unusual peritoneal investment. Eastman has indicated this especially in relation to Treves's fold. In this connexion he gives another interpretation of C. H. Mayo's view regarding the congenital origin of Jackson's membrane. These are the various ways in which such a membrane may be formed apart from pathological causes. I have an interesting specimen showing the genito-mesenteric fold forming a partial investment for the ascending colon.

By the term "adhesion" I mean a union which was not different from those which occur elsewhere during the fusions together of peritoneal sheets in the fœtus. Moreover, I have shown that there is no "general shifting of the endothelial layers in such a manner that what was once free peritoneal surface remains free"; and have demonstrated the mechanical causes which operate in producing adhesions in different situations.

[3] In children "numerous instances of acute and chronic salpingitis, sometimes accompanied with ovaritis and pelvic peritonitis, have been recorded" (Kelly, *Operative Gynecology*, 1906, vol. ii. p. 566).

"Appendicitis occurs so frequently that it should be formally designated as a disease of childhood (Sonnenberg, Karewski, Selter)" (Pfaundler and Schlossmann, *The Diseases of Children*, vol. iii.).

[4] For other photographs of the genito-mesenteric and other folds of peritoneum, etc., see my paper in the *Proceedings of the Royal Society of Medicine*, February 1914, and Professor Eastman's paper, "Fœtal Peritoneal Folds" (*Journal of the American Medical Association*, 30th August 1913).

point 2 cm. from the internal abdominal ring (annulus inguinalis abdominalis) it deviated from this line and passed horizontally outwards for 1·2 cm. The fold thus formed a shelf (I have seen it forming a deep pocket), slightly concave upwards, upon which the appendix rested at the lowest point of its acute curve convex downwards (see fig. 3).

There was no doubt that this alteration in the line of attachment was brought about through the pressure which had been exerted upon the left

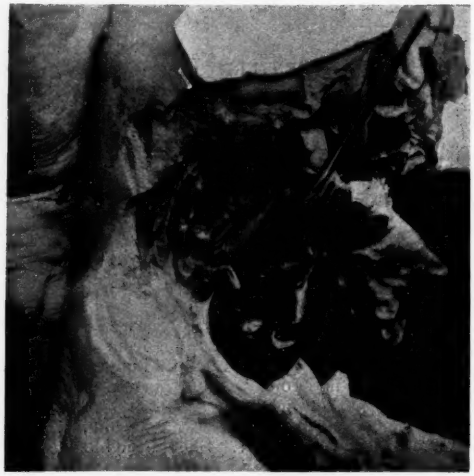

FIG. 3.—Full-time fœtus No. I. The specimen is viewed from the right side. An opening (above which lies the ileo-cæcal orifice) has been made into the cæcum. The ileum is simply steadied by the hook, and the natural form of the loop is in no way distorted (*cf.* fig. 4). Note the large loop of pelvic colon to the left of the genito-mesenteric fold.

surface of the fold by the large intra-abdominal meconium-distended pelvic colon.

I have now noted, in a number of fœtuses, that the pelvic colon may obliterate in this way part of the genito-mesenteric fold, and thus interrupt a track by which inflammation may spread from the bowel to the ovary and Fallopian tube, or in the opposite direction. The appendix at first descended for a distance of nearly 2 cm.; and in this part of its course skirted the posterior border of the genito-mesenteric fold, and adhered firmly to the posterior abdominal wall, as did the cæcum higher up.

Below, where it became bent upon itself to form an acute flexure, it was bound directly to the right surface of the fold.

The ileum, as traced from the ileo-cæcal junction, also descended for 2 cm. and then ascended for the same distance. It thus formed a loop (see fig. 3). This was firmly bound, *throughout its entire extent*, to the right surface of the genito-mesenteric fold.

FIG. 4.—Another view of the genito-mesenteric fold in full-time fœtus No. I. Whilst this photograph was being taken, a slight traction, in an outward direction, was exerted upon the ascending limb of the loop of ileum (indicated by the thread and the strip of white paper). The exact position of the posterior (parietal) border of the fold is indicated by the end of another strip of paper.

Not only this, the mesentery of the loop also adhered to the right side of the fold, as did the whole of the meso-appendix. Therefore the appendix was connected to the terminal part of the ileum not only by the bloodless fold of Treves, also fused down, but by the meso-appendix and genito-mesenteric fold. Its lymph-vessels were thus thrown into immediate connexion with those of the ileum and genito-mesenteric fold—a connexion which is not uncommon, however, as the ileum quite frequently adheres to

the fold and is then often connected with the meso-appendix, over which the ileum also frequently fuses down to the abdominal wall.

I have pointed out (*Proceedings of the Royal Society of Medicine*, February 1914) that it is necessary to distinguish between flexures of the terminal part of the ileum which are permanent and those which have no real claim to be regarded as other than temporary, and also (*Journal of Anatomy and Physiology*, 1909–13) that the ileum, appendix, cæcum, etc., may adhere to the genito-mesenteric fold. But fœtus I. (see figs. 3 and 4) was especially interesting in that the ileum and appendix *both* adhered to the fold *and formed flexures which were rendered permanent* in this remarkable manner. In another full-time fœtus there was an almost exactly similar condition.

In several fœtuses I have observed that the appendix may lie completely below the cæcum; and when retained in this position by a genito-mesenteric fold, it is noteworthy that it may become retro-colic if the cæcum is able to complete its descent.[1]

In two full-time fœtuses the appendix, besides adhering to the right surface of the genito-mesenteric sheet, was bent backwards over its sharp free edge to come into contact with the left surface of the fold. The appendix and its mesentery may be acutely kinked in this way; and if kept thus for any length of time, or should the kink become permanent, inflammation, or even strangulation, may follow upon interference with the blood supply. I have pointed out that the genito-mesenteric fold may in some cases determine strangulation of the ileum.

In fœtus II. (see fig. 5) the genito-mesenteric fold passed downwards from the mesentery, and ileac branch of the ileo-colic artery, to the Fallopian tube and ovary. Lying in the fold, some in its central part, others close to its mesenteric border, were a number of small lymph-nodes —an important point. It contained many blood-vessels, especially veins —some of these could be traced to the ovarian vein. Apart from these vessels, no muscular fibres were present in the part removed for microscopic examination.[2] The meso-appendix adhered to the right side of the fold (to a much greater extent than would appear from the photograph).

This important connexion is very common. Indeed, when there are no adhesions binding the ileum, meso-appendix, etc., to the abdominal wall, the two folds are rarely seen completely separate from one another.

The ileo-appendicular fold of Jonnesco ("bloodless" fold of Treves) was

[1] For photographs showing variations in the position and relations of the appendix at different stages of cæcal torsion, see my paper in the *Proceedings of the Royal Society of Medicine*, February 1914. Such variations must of course be interesting to the surgeon.

[2] It might be well to make further microscopic examinations of folds in fœtuses at various ages.

quite distinct from the genito-mesenteric fold, with which it should not be confused (see fig. 5).

The genito-mesenteric fold may remain well marked in the adult; but even if obliterated, through fusion with adjacent peritoneum, it must "leave behind," in the form of adhesions, many permanent results of its presence.

A remnant of the fold was present this term (Lent, 1914) in two out of six adults (33 per cent.).

In both it was attached to the peritoneum over the external iliac artery.

FIG. 5.—Full-time fœtus No. II., ♀. The genito-mesenteric fold is viewed from the right side. One strip of white paper crosses the appendix, and the others indicate the posterior border of the fold and the upper end of the Fallopian tube. Note the ileo-appendicular fold of Jonnesco ("bloodless" fold of Treves).

In one it passed from the terminal part of the ileum, at the lower limit of the adhesions (present in 50 per cent. of adults), binding this to the peritoneum of the iliac fossa. These adhesions were absent in the other case, the fold passed from the mesentery, and the meso-appendix adhered to its right surface. The root of the mesentery formed an angle the vertex of which lay at the genito-mesenteric fold, and considerably below and to the left of the ileo-colic artery (which primitively lies along the line of the root). The root descended, much more vertically than usual, to reach the fold. It then passed to the right and slightly downwards to a

normally placed cæcum. Obviously *the genito-mesenteric fold had caused an abnormal displacement of the root of the mesentery downwards and to the left.*[1]

In accounting for the adhesions in the ileo-cæcal region, not only the genito-mesenteric fold, but the large intra-abdominal pelvic colon, so often seen in the fœtus, and the relatively unyielding posterior and right lateral abdominal walls must be kept in mind.

Thus, confined between the abdominal wall and the genito-mesenteric fold, and rendered relatively immobile through the anchoring of the mesentery and connexion with the large intestine, the terminal part of the ileum, as well as the mesentery on each side of the fold, may readily become adherent to adjoining peritoneum against which it is pressed.

The pressure exerted by the pelvic colon is important in determining adhesions.[2] Special attention is directed to this mechanical cause of peritoneal adhesions. The cæcum and appendix may be bound directly to the abdominal wall or, in the case of the appendix, to the under surface of the mesentery, as a result of this pressure. This gives us an explanation, apart from pathological causes, of the direct adhesion, sometimes seen in adults, of the appendix and meso-appendix, to the left (under) surface of the mesentery. The whole appendix may become "sessile" in this way and may be kinked acutely and permanently. Adhesions involving the pelvic mesocolon itself may thus be produced (see the *Journal of Anatomy and Physiology*, 1911, vol. xlv.).

I have now shown that we are further justified in believing that the genito-mesenteric fold must be of interest to the surgeon and gynecologist, not only as a track by which infection or inflammation may spread, but in relation to the formation of adhesions—adhesions which may act as ready-made barriers resisting the spread of inflammation, adhesions which the surgeon may encounter, and should carefully deal with, in operations in the ileo-cæcal region.

(*c*) The Supra-Adhesion Foramen.

I have already published figures and a photograph of this foramen (see the *Journal of Anatomy and Physiology*, July 1911 and 1912, April 1913, and the *Proceedings of the Royal Society of Medicine*, February 1914) as

[1] In association with the fold in the fœtus, whilst the cæcum still lies high up in the abdomen, I have shown that the root of the mesentery may acquire the direction it normally has in the adult.

[2] It is noteworthy that if in the fœtus a large unyielding meconium-distended pelvic colon remain with its summit at the level of the duodenum, the mesentery may fuse down over this part of the colon. I have noted this in several adults. I have a photograph showing some remarkable effects of the pressure exerted upon adjacent parts by the pelvic colon.

FIG. 6.—The supra-adhesion foramen in an adult, ♀. The liver has been pulled upwards and the gastro-hepatic omentum reflected downwards. The handle of the knife rests upon the stomach at its pyloric end, and the blade lies in the foramen. Photo by Mr Walter J. Calcott, Anatomical Museums, Cambridge.

FIG. 7.—The supra-adhesion foramen in a fœtus (♂) 19 cm. long. A large portion of the liver, and the left part of the great omentum have been removed and the greater curvature of the stomach has been pulled upwards into contact with the heart. Note how the transverse mesocolon passes from the stomach below the small foramen. Behind the foramen the "deep gastric ligament" is seen. Photo by Mr W. J. Calcott.

seen in fœtuses. Fig. 6 shows the foramen as I have frequently seen it in adults.

The coronary vein lay at some distance from the free margin of the coronary (left gastric) portion of the septum bursarum omentalium (deep gastric ligament of Jonnesco, plica gastro-pancreatica).

Primitively it lies along this border. Fig. 7 shows how the foramen is determined, viz. by adhesions (appearing relatively late in intra-uterine life) which bind the postero-inferior surface of the stomach to the transverse mesocolon. These and other adhesions must be of importance both in anatomy and surgery in helping to fix and support the viscera.

THE ANATOMY OF THE HEAD END OF A 20-MM. HUMAN EMBRYO.

By J. K. Milne Dickie, M.D., F.R.C.S. Edin., *Demonstrator of Anatomy, University of Edinburgh.*

The embryo here described is in the collection of the University of Edinburgh. It was removed by operation and was fixed in a 5 per cent. aqueous solution of formaldehyde. After fixation the vertex-breech measurement was 20 mm. There are no data as to its age, but, judging from its length and general development, it may be placed at approximately a little over seven weeks. The specimen was stained in bulk with acid hæmalum and eosin, and cut in serial transverse sections of 10μ. A series of models of the head region, at a magnification of 50 diameters, was reconstructed by the wax-plate method. It is upon these models that the following description is based.

The general characteristics of the embryo are very similar to those of others of about the same age, of which records have been published, and which are figured in Keibel's *Normentafeln* (1). The cervical flexure is still so well marked that the chin almost touches the chest wall. The outlines of the brain can be easily distinguished through the superficial tissues (fig. 1). The head in the region of the hind-brain is somewhat wrinkled, but its outline presents a fairly uniform curve, while in Meyer's 18·5-mm. embryo (1) the hind-brain forms a distinct projection. The external acoustic meatus is represented by a deep oval pit. Its edges are raised and thickened, but there are no longer any distinct tubercles. It is similar to embryos of 18 and 18·5 mm. in the *Normentafeln*, while in embryos of 20 and 22 5 mm. the cavity of the meatus is much diminished. The forehead is a large rounded prominence, separated from the nose by a deep transverse fronto-nasal groove, which is prolonged laterally into the upper eyelids. The eyelids are still widely separated. They are better defined than appears to be the case with some other embryos of comparatively similar age, for they are thick raised folds surrounding the eye. The other eyelid is groved by the lateral continuation of the fronto-nasal groove, which divides it into three segments, viz. a small triangular part at the medial commissure (fig. 1, A), a larger intermediate part (B), and a lateral part (C), which becomes continuous with the lower lid at the lateral commissure. The lower lid is smooth, and blends with the

cheek and the upper lip at the angle of the mouth, and is continuous medially with the root of the nose. The nose is broad and upturned. The nares are widely separated and directed forwards (fig. 2). Their openings are small and partly occluded by plugs of epithelium. They are bounded laterally by thick alæ nasi. The mouth is open, exposing the tip of the tongue. The upper lip has a shallow median notch. The lower lip is a smooth rounded shelf, with no trace of its bilateral origin. There is a distinct double chin, which is seen also in an embryo figured by His (2).

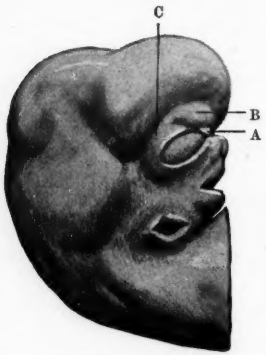

FIG. 1.—Profile view of the embryo showing general form.

FIG. 2.—Front view of embryo.

NERVOUS SYSTEM.

Brain.—The three flexures of the brain are still well marked, the cephalic flexure forming the most acute angle of the three.

Primitive Forebrain and its Divisions.—The primitive forebrain is distinctly separated into telencephalic and diencephalic portions. The telencephalon has divided into two cerebral hemispheres, and each hemisphere, which is ovoid in form, has grown ventrally (forwards) beyond the lamina terminalis and dorsally (backwards) over the antero-superior portion of the diencephalon (fig. 3). The olfactory bulb on the ventral surface of the hemisphere is distinctly defined, and is limited medially and posteriorly by a sulcus. In sections it is seen to be definitely connected with the olfactory epithelium by nerve fibres. The eye stalk on each side is attached to the end of the forebrain, about half-way between the olfactory bulb and the hypophysis. It is very slender, and shows no trace of its originally hollow character. The eye stalk of Keibel's 18-mm. embryo (1) also is solid, but that of Meyer's 18·5-mm. embryo is still to a great extent pervious. There is as yet no chiasma. The hypophysis is

situated at the ventral corner of the forebrain and is flattened dorso-ventrally. The buccal lobe is crescentic in form and partly surrounds the smaller infundibular lobe. It is hollow and still connected with the mouth by a thin cord of cells.

The lateral wall of the third ventricle is distinctly separated by a hypothalamic sulcus into a dorsal thalamic and a ventral hypothalamic region. The hypothalamic sulcus pursues a curved course from the interventricular foramen round the thalamus, and is continuous with a furrow which traverses the entire length of the mid-brain. The optic recess bounds the hypothalamus anteriorly, and intervenes between it and the corpus striatum. The corpus striatum, again, is separated from the thalamus by the anterior part of the hypothalamic sulcus, and is prolonged laterally

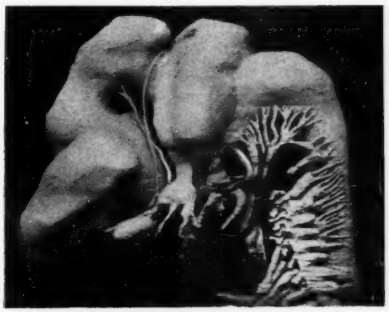

FIG. 3.—Lateral surface of model of brain and cranial nerves.

through the interventricular foramen of Monro to form part of the floor of the lateral ventricle. The interventricular foramen is a wide opening, through which one can see a large choroid plexus in the lateral ventricle. The hypothalamus is separated by a shallow sulcus into an anterior and a posterior portion. The anterior portion lies just dorsal to the hypophyseal recess, while the posterior part becomes continuous with the floor of the mid-brain. The posterior part of the floor of the diencephalon forms a projection outwards, representing the mammillary protuberance. The thalamus is crossed by a ridge which separates it into dorsal and ventral portions. The posterior or caudal end of this ridge is lost on the lateral wall of the ventricle on a level with a recess in the roof, which probably represents the pineal recess. The anterior end of this ridge is joined by a prominent fold attached to the roof of the diencephalon. Its anterior end blends with the thalamus, and its surface is continuous through the interventricular foramen with the choroid plexus of the lateral ventricle. This fold is seen in several of His's specimens (3), and is most probably the

commencement of the choroid plexus of the third ventricle, since, according to Elliot Smith (4), that structure is developed from the roof of the forebrain. This choroid ridge extends posteriorly along the roof of the forebrain to a point opposite to where the floor becomes invaginated just posterior to the mammillary eminence. Immediately caudal to its posterior extremity the roof is thickened, and in this thickened portion of its wall are two recesses, which may represent the pineal and prepineal recesses. The anterior commissure is represented by a thickening of the lamina terminalis about its middle.

Mid-brain.—The mid-brain or mesencephalon is tubular and curves on itself to join the isthmus. Viewed from the lateral aspect it is somewhat indistinctly separated into a lamina quadrigemina and a peduncular

FIG. 4.—Shows medial aspect of model of brain.

i, Cerebellum; ii, tegmentum; iii, thalamus; iv, interventricular foramen; v, olfactory bulb; vi, vagus; vii, sympathetic.

portion. The dorsal part of lamina quadrigemina projects posteriorly over the isthmus so as almost to touch the roof of the fourth ventricle. The cavity of the mid-brain is much smaller than that of the forebrain. Its roof shows several irregularities, probably artificial, as this region of the brain was somewhat damaged. The floor of the mid-brain is thickened on each side of the middle line, this thickening represents the tegmentum of the adult, and is bounded laterally by the continuation of the sulcus hypothalamicus. At the isthmus a small deep pit is seen in the lateral wall.

Hind-brain.—The hind-brain has still distinct pontine and cervical flexures. Its walls vary considerably in thickness in different portions. The thin roof of the fourth ventricle bulges upwards and also laterally, and forms a very prominent feature of the brain in this region. Near the cervical flexure the choroid plexus forms a deep transverse invagination

of the roof, and divides it into anterior and posterior portions. The anterior portion of the roof overlaps the alar lamina of the anterior limb of the pontine flexure, so that a deep sulcus appears on the outer surface running parallel with the anterior limb of the pontine part of the brain. The posterior part of the roof of the fourth ventricle is not nearly so prominent as the anterior part, and blends with the medulla oblongata, which tapers off rapidly into the spinal medulla. The diameter of the spinal medulla is fairly uniform, but opposite the origin of the brachial nerves it increases somewhat in thickness. The spinal medulla in the cervical and upper thoracic regions is nearly straight, there being only a slight ventral convexity. The appearance of the hind-brain, as seen from inside, is very striking. The cavity of the fourth ventricle communicates with the mid-brain by means of a narrow isthmus rhombencephali. Immediately posterior to this the cavity widens out in all its diameters. Its floor is very thick, especially in the posterior limb of the pontine flexure and in the region of the medulla oblongata It has a longitudinal ridge on each side of the middle line which traverses the whole length of the hind-brain. The alar lamina is distinctly separated from the basal lamina in the anterior part of the pons by a furrow. It forms a thick rolled edge and has three bends on it. It begins on the lateral wall of the isthmus near its roof and runs laterally and dorsally a short distance. It then bends at an acute angle and runs ventrally a short distance. Soon it bends slightly laterally, and then again resumes its ventral direction till it reaches the pontine flexure, where it ends. It is much thicker at its pontine end than at the isthmus. Lateral to it the roof forms a very deep recess. The part of the ventricle posterior or caudal to the choroid plexus is comparatively shallow. It is broad at its anterior end, but narrows rapidly into the central canal of the spinal medulla. The cervical flexure occurs in this part of the brain, hence the floor of the cavity is convex in the sagittal plane.

The Spinal Medulla.—The spinal medulla has a large central canal, narrow from side to side, but wide in the sagittal plane. The ventral wall is much thicker than the dorsal wall. Its ventral surface shows a shallow median groove. Transverse sections show that the greater part of the spinal medulla is composed of grey matter with a surrounding zone of white matter.

Cranial Nerves.

I. The olfactory bulb on each side is represented by a short, thick process from the ventral surface of the cerebral hemisphere, extending between it and the epithelium of the dorsal part of the olfactory cavity.

It is composed of a more or less homogeneous mass of cells with round or oval nuclei.

The optic nerve on each side is fairly slender and springs from the corresponding angle of the diencephalon. It consists largely of cells, but mixed with them are a number of longitudinal fibres, which can be traced as far as the junction of the optic stalk with the diencephalon. There is as yet no indication of any fibres crossing the middle line to form a chiasma. There is now no cavity in the interior of the optic stalk. Keibel's 18-mm. embryo also has a solid optic nerve, while the nerve of Meyer's 18·5-mm. embryo is still hollow.

III. The oculomotor nerve is very long. It arises from the floor of the mid-brain by a bunch of five or six fine rootlets, and passes ventrally between the forebrain and the hind-brain till it comes into relation with the semilunar ganglion, when it curves laterally between the ophthalmic and maxillary divisions of the trigeminal nerve to end in the neighbourhood of the eye.

IV. The trochlear nerve springs from the root of the isthmus by a single root. It arches round the mid-brain and passes forwards a little lateral to the oculomotor nerve. Near the eye it curves forward in intimate relation to branches of the trigeminal nerve, and ends near the olfactory bulb.

V. The trigeminal nerve arises as a very thick trunk a little anterior to the apex of the pontine flexure and some distance from the median plane. Soon after leaving the brain it expands into the large semilunar ganglion, which at this stage is somewhat triangular in shape. At its central or proximal end the nerve consists mainly of fibres, with which a few cells are intermingled; but as the triangular enlargement which represents the semilunar ganglion is approached, the cells increase in number, more especially round the periphery of the bundle of fibres. As the more distant part of the ganglionic mass is approached, the cells increase in number until they almost entirely replace or conceal the fibres. Along the medial side of the ganglion a small bundle of fibres remains distinct, and can be traced into the mandibular division of the nerve. This bundle represents the motor root.

The ophthalmic division springs from the extreme frontal end of the ganglion and runs obliquely downwards and forwards. It soon divides into two branches, one passing medial to the eyeball to end near its medial commissure, the other ending near the optic nerve.

The maxillary division consists of a single trunk, passing downwards and forwards just under the eye to end in the cheek.

The mandibular division (fig. 5), the largest branch of the trigeminal,

springs as a short thick trunk from the posterior angle of the semilunar ganglion. It passes downwards (caudally) for a short distance before breaking up into its various branches. Of these, the most medial is the lingual nerve, which passes in a medial direction as a flattened band to reach the side of the tongue, where it enlarges into a ganglion just lateral to the submaxillary gland. The auriculo-temporal is the most posterior branch, and is much smaller than the lingual nerve. It has a short course, curving laterally to reach the skin round the external acoustic meatus. The inferior alveolar nerve lies at first anterior to Meckel's cartilage, but gradually comes to assume a position lateral to it, and is continued on into the chin region. During its course it gives off a small branch, which

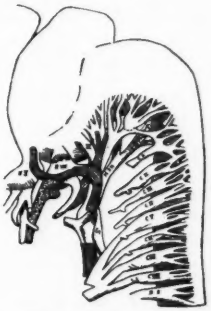

FIG. 5.—Sketch of nerves in occipital region. Meckel's cartilage is stippled. The lateral head vein and part of the internal jugular vein are also shown.

crosses Meckel's cartilage on its lateral side and ends in the mylohyoid muscle. The nerve to the masseter lies lateral to the inferior alveolar nerve and ends in the masseter muscle. The buccinator nerve lies just under cover of the epithelium at the angle of the mouth.

VI. The abducent nerve arises from an area medial and slightly caudal or posterior to the trigeminal and on the same level as the facial nerve by a bunch of small rootlets. It passes downwards and forwards towards the eye, and then curves laterally between the ophthalmic and the maxillary divisions of the trigeminal.

VII. The facial nerve comes from the ventral surface of the brain slightly medial to the acoustic nerve, and curls round its anterior border so as to lie in a groove in its lateral surface. Leaving the acoustic nerve, it develops a small geniculate ganglion and runs in a caudal direction for some distance, crossing over the long process of the incus, which at this

stage lies horizontally. Soon after this it bends downwards and gives off the chorda tympani, which passes between the malleus and the long process of the incus to reach the lingual nerve. The facial nerve now gives off the nerve to the digastric and passes on to its distribution in the face.

VIII. The acoustic nerve is connected with the pontine part of the hind-brain by two roots. The more medial of the two is the mandibular root, the more lateral is the cochlear root, which, as it enters the brain, becomes associated with a group of cells which represent the dorsal and ventral cochlear nuclei. Outside the brain the two roots are in close apposition. The peripheral end of the trunk becomes associated with a group of cells which is in process of separation into the spiral ganglion and the smaller vestibular ganglion.

IX. The glossopharyngeal nerve lies in series with the vagus and accessory nerves on the lateral aspect of the hind-brain. It arises as a single thick trunk, which expands slightly to form the superior ganglion. It passes down ventral to the vagus, and, at the level of the auditory ossicles, it shows a much larger petrous ganglion, which gives off from its ventral side a small twig—the tympanic nerve of Jacobson. Below this point it curves forwards and medially to the tongue.

X. and XI. The vagus and accessory nerves arise by means of a long series of rootlets, which spring from the side of the hind-brain along a line corresponding in direction with the cervical flexure. These run together to form a single large trunk. The spinal root of the accessory can be traced down on the medial side of the cervical nerves as far as the rootlets of the third cervical ganglion. Numerous small ganglionic swellings are seen on the rootlets before they unite to form the vago-accessory trunk. At the upper part of the trunk is a collection of cells which represents the jugular ganglion, and at a lower level the fibres of the trunk become intermingled with cells of the ganglion nodosum. Some of the most caudal rootlets communicate with the first cervical ganglion, and at the point of junction a small ganglion of Froriep is seen. The vago-accessory trunk passes down ventral and lateral to the vertebral column, and opposite the second, third, and fourth cervical vertebræ is the ganglion nodosum, which has been already mentioned. This ganglion is large and spindle-shaped, and gives off from its medial aspect a short superior laryngeal nerve, which passes straight into the larynx. The vagus is continued down into the thorax dorsal to the pericardium.

XII. The hypoglossal nerve arises in a plane medial to the vagus and accessory nerves and in series with the spinal anterior nerve-roots. Its eight or nine slender roots fuse to form a flattened trunk, which comes to lie in contact with the dorsal surface of the ganglion nodosum. It then

winds round the ganglion nodosum in a groove on its lateral surface. From this point it turns forwards and medially to the root of the tongue. A descending branch is given off, which accompanies the vagus nerve some distance further.

The first cervical nerve has a small ganglion, which forms communications with the roots of the vago-accessory nerve and with the second cervical nerve. The other cervical ganglia are much larger. The anterior roots are not easily seen. As the nerves emerge from the intervertebral foramina each gives off a small posterior branch. The lower cervical and upper thoracic nerves converge as they leave the spinal medulla and unite to form the brachial plexus.

The sympathetic gangliated trunk in the middle of the neck lies dorsal to the vagus. As it is followed towards the head it comes to lie medial to the vagus, and at the level of the petrous ganglion of the glossopharyngeal nerve it turns abruptly forwards with the carotid artery in the direction of the forebrain. As the trunk is traced towards the thorax it gradually diverges from the vagus, but is still dorsal to it. At the level of the seventh cervical vertebra it forms a loop and is continued into the thorax.

Streeter (5) has reconstructed the nerves in the occipital region of a 17·5-mm. embryo. In most respects the anatomy is very similar to the embryo here described. There are, however, some points of difference—thus in Streeter's specimen the glossopharyngeal nerve arises by several rootlets, and the gangliated trunk of the sympathetic fuses with the ganglion nodosum of the vagus. In this embryo the glossopharyngeal arises by a single root, and the sympathetic is separate from the vagus. The rootlets of the spinal ganglia in Streeter's embryo are much shorter than in mine.

Vascular System.—The carotid artery passes up the neck medial to the vagus, and opposite the first cervical vertebra it curves forwards in the direction of the forebrain. The stapedial artery is present and passes through the hole in the stapes. The two vertebral arteries unite in the concavity of the cervical flexure to form the basilar artery, which at this stage is a long vessel following closely the ventral surface of the pons as far as the cephalic flexure.

The blood from the frontal end of the brain is conveyed by the anterior cerebral veins into the large primitive head vein, which lies medial to the semilunar ganglion and represents the future cavernous sinus. Here it receives a small tributary from the region of the hypophysis. At the posterior edge of the semilunar ganglion it is joined by the middle cerebral vein, which drains the mid-brain and roof of the fourth ventricle. The

large vessel (vena capitis lateralis) thus formed is continued posteriorly, lying immediately lateral to the facial nerve and accompanying it out of the cranium. It now lies lateral to the IX., X., XI., and XII. nerves. Opposite to the vagus it receives a large tributary (posterior cerebral vein) from the medulla oblongata, and emerges from the cranium by an opening which later becomes the jugular foramen. The vena capitis lateralis now turns sharply downwards and accompanies the vagus nerve on its lateral aspect, where it becomes the primitive jugular vein.

In the earliest stages of development the frontal part of the primitive head vein is represented by the vena capitis medialis, which lies medial to the cranial nerves. Later on loops are thrown round the nerves and the medial part disappears, transforming the vessel into the vena capitis lateralis. This series of changes has been fully worked out by Salzer (6) in guinea-pigs, and by Grosser and Brezina (7) in reptiles. Rabl (8) has pointed out that in selachians the persistence of the vena capitis medialis is the normal condition, though in *pristiurus* there are both medial and lateral vessels. The vena capitis lateralis is identical with the "Basalvene" described by His (3).

This embryo shows an intermediate stage in the development of the veins of the head. The early vena capitis medialis has been entirely replaced by the vena capitis lateralis, with the exception of that part medial to the semilunar ganglion, which persists as the cavernous sinus. Later the three cerebral veins anastomose and the vena capitis lateralis atrophies and disappears, so that all the blood leaves the cranium through the jugular foramen (Mall, 9).

The Upper Air-Passages.

The buccopharyngeal cavity (fig. 6) is widest at the angle of the mouth. From this point backwards it narrows rapidly to the level of the middle ear recess, where it again widens, and behind which it tapers away gradually into the œsophagus, the lumen of which is uniformly narrow. The cavity as a whole is curved on itself, with a ventral concavity, to the extent of about half a circle. In the roof the primitive choanæ are seen as oval openings. The primitive palate, *i.e.* that part of the roof of the mouth between the lip margin and the choanæ, presents a shallow groove, the labio-dental sulcus, which runs parallel to the lip margin. The epithelium on the floor of this groove is somewhat thickened. The palatal processes commence from the primitive palate at the anterior end of the choanæ, form the lateral boundary of the choanæ, and are continued backwards along the roof of the mouth till they reach the medial surface of the mandibular arches, which they cross and fade away on the anterior

wall of the first cleft, which at this stage is becoming the lateral wall of the middle ear recess.

The middle ear recess is a wing-shaped extension from the side of the pharynx (fig. 6). Its upper wall or roof shows a convexity caused by the tip of the cochlea. There is an antero-lateral wall and a postero-lateral wall separated by a deep cleft, which corresponds with the angle between the first and second arches. The body of Meckel's cartilage bulges into the antero-lateral wall, while the handle of the malleus similarly causes a bulging on the postero-lateral wall. The most anterior or oral end of the middle ear recess is in the form of a narrow cleft, which runs from the

FIG. 6.—Model of the upper air-passages. Nasal cavities form top of model. At the side is a groove corresponding with palatal process. Further down middle ear recess is seen, and beyond that the cavity narrows into the œsophagus.

i, Palatal process; ii, sulcus tubo-tympanicus; iii, eminentia cochlearis; iv, second visceral pouch.

tympanum forwards and medially along the roof of the buccopharyngeal cavity. This cleft has been named by Hammar (10) and others the sulcus tubo-tympanicus. It is bounded laterally by the continuation backwards of the palatal process on the lower and posterior surface of the mandibular arch. Its medial boundary is the eminentia cochlearis.

The dorsal extension of the second pouch can be distinguished as a shallow pocket in the posterior edge of the middle ear recess, where it opens on to the pharynx (fig. 6). None of the other pouches or clefts can be distinguished in the lateral wall of the pharynx.

The parotid gland is represented by a solid bud of epithelium, growing into the cheek just behind the angle of the mouth. The submaxillary

gland is also a solid bud of epithelium, growing downwards from the bottom of the alveolo-lingual sulcus. The sublingual gland has not yet appeared.

In the margin of the lower lip there is a labio-dental sulcus similar to that in the upper lip. The tongue occupies most of the floor of the mouth. Its tip reaches nearly to the lip margin, and is bound down by a short frenum. The organ is long and narrow, with a shallow median groove. It is sharply defined from the floor of the mouth by a deep alveolo-lingual sulcus. The root of the tongue can be faintly distinguished from the rest by a shallow transverse groove. There remains no indication of the relative parts played by the tuberculum impar and the lateral tongue rudiments, the anterior two-thirds of the tongue being quite uniform and smooth.

The epiglottis is a thick transverse ridge behind the root of the tongue. The upper aperture of the larynx is bounded behind and laterally by two rounded arytenoid swellings, which are in close apposition to the epiglottis and each other, so that the interval between them is a T-shaped cleft. Below this point the anterior laryngeal wall presents no special features. The laryngeal cavity consists of a transverse and a sagittal part. The transverse cleft is bounded behind by the arytenoid swelling and in front by the epiglottis, and the sagittal cleft lies between the two arytenoid eminences. A large part of the transverse cleft becomes the superior laryngeal aperture of the adult, the arytenoids later becoming separated from the epiglottis. The sagittal cleft is for the most part only a potential cavity, the two arytenoid swellings lying in close apposition, leaving only a narrow channel posteriorly. Lower down the sagittal part of the cavity opens out, the lumen being at first triangular, then oval as it passes into the trachea. There is as yet no trace of the chordal tubercle described by Frazer. The laryngeal cartilages are represented by condensations of precartilaginous tissue.

The Nose.—The nasal cavities open in front by the anterior nares and communicate with the buccal cavity by means of primitive choanæ, which are oval openings in the roof of the mouth. Their greatest diameters are in the antero-posterior direction. The anterior nares are narrow, and their lumina are almost entirely occluded by epithelial plugs, as is usual at this stage. Behind this point the cavity increases rapidly in its vertical diameter. The floor slopes down from the anterior orifice to the anterior border of the choana, and is formed entirely by primitive palate; while the roof runs first upwards and backwards, and then arches downwards to the posterior end of the choanal orifice. The lateral wall (fig. 7) is as yet fairly simple. Near its lower boundary there is a rounded swelling repre-

senting the concha inferior. This is limited below by a furrow, with which the solid naso-lacrimal duct is connected. The infundibulum ethmoidale is represented by a deep oblique cleft in the lateral wall near its roof. Immediately above and behind this the first ethmoturbinal is seen on the roof of the cavity. This illustrates a stage of the process described by Peter (11), in which the ethmoturbinals, which are originally on the medial wall, migrate across the roof on to the lateral wall. On the medial wall of the nose (fig. 8) is an antero-posterior sulcus, situated about midway between the floor and the roof. It deepens as it passes back to become a pocket, and obviously represents part of Jacobson's organ. In the region of the pocket the epithelium is thick and columnar, and nerve fibres can

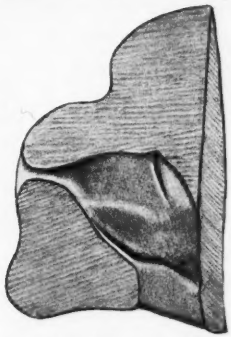

FIG. 7.—Lateral wall of the nasal cavity showing the concha inferior, the commencement of the infundibulum ethmoidale, and the first ethmoturbinal.

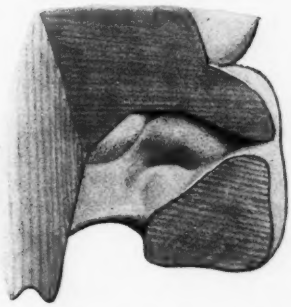

FIG. 8.—Medial wall of nose showing Jacobson's organ and one of the ethmoturbinals.

be traced from it to the olfactory part of the brain. In the upper and posterior part of the septum there is a small bulging area, probably representing the second ethmoturbinal.

The Eye.—The retina is a cup-shaped structure formed of two layers, which are as yet distinct. The outer layer already contains some pigment. The hyaloid artery is still present. The lens is a spherical mass lying in the retinal cup. It still shows a crescentic cavity in its interior.

The extrinsic muscles of the eye are just beginning to appear, and are still in a very rudimentary condition.

I have been unable to discover in this embryo any trace of a lacrimal gland, although there is a well-developed conjunctival sac both above and below. The naso-lacrimal duct is present as a solid column of cells, which arches in from the medial commissure to the inferior meatus of the nose.

The Labyrinth.—The labyrinth as a whole is situated slightly dorsal to the external acoustic meatus. Its oral or ventral extremity is formed by the cochlea, the saccus endolymphaticus is its most dorsal extremity, while the vestibule occupies an intermediate position.

The cochlea (figs. 9 and 10) is beginning to show a constriction at its junction with the vestibule, but the ductus reuniens so formed is as yet very wide. The ductus cochlearis is short and thick, and of its windings only two-thirds of a turn are completed. It lies very close to the middle ear recess and causes a bulging into its roof, as already mentioned.

The vestibule is somewhat elongated, and shows on its medial surface two rounded projections, which represent the beginning of the differentiation into saccule and utricle.

FIG. 9.—Lateral aspect of the membranous labyrinth.

FIG. 10.—Medial aspect of the membranous labyrinth. The commencing separation into utricle and saccule is seen.

The semicircular canals or ducts are well developed and occupy the same relative positions to one another as they do in the adult. The ampullæ are already evident. The lateral or horizontal canal is considerably shorter than the superior or posterior semicircular canal.

The ductus and saccus endolymphaticus are represented by a spear-shaped diverticulum from the vestibule, medial and parallel to the crus commune.

Streeter (12) has reconstructed and described the labyrinth of a 20-mm. human embryo, which corresponds in every respect with the specimen described in this paper.

Branchial Derivatives.—The thyroid gland is a U-shaped structure. The limbs of the U are flattened at their cranial ends, but as they are followed downwards they become more rounded and meet in the middle line in front of the trachea. The upper or cranial extremities lie lateral

to the lower part of the pharynx, though they have no connexion with it. The thyro-glossal duct has also completely disappeared. The thyroid is seen to be composed of loosely-connected columns of deeply-staining round cells. There is no distinct capsule. The thymus is in the form of two rounded cords, which lie close to the vagus carotid. Each cord begins about the level of the third or fourth cervical vertebra, just lateral to the thyroid gland, ventral to the carotid, and medial to the vagus. It passes down the neck, preserving these relationships, and comes gradually forwards towards the middle line, and unites with its fellow of the opposite side in front of the aortic arch. It is a mass of deeply-staining, closely-arranged cells. It has a definite capsule, and, in the greater part of its length, a narrow lumen.

The Skeleton.—The base of the skull is composed of precartilaginous tissue, with here and there chondrifying centres. The outlines are as yet somewhat indefinite.

The vertebræ are mostly cartilaginous, while the spaces between the bodies of the vertebræ are filled up by condensed tissue, not unlike cartilage in appearance. The vertebræ and intervertebral substance form a continuous column in front of the spinal medulla. The neural arches are quite open dorsally, the laminæ extending only about half way round the spinal medulla. The transverse processes are flattened and are pierced by the canal containing the vertebral artery.

The notocord runs up the centre of the vertebral column into the base of the skull. It then bends ventrally, and, emerging from the base of the skull, travels forwards between the mucous membrane of the pharynx and the base of the skull to end near the hypophysis.

In conclusion, I wish to express my thanks to Professor Robinson for placing his specimen at my disposal, and for much valuable advice.

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ANATOMICAL NOTE.

A New Roller for Making Wax Plates. By Professor Fawcett, *University of Bristol.*

This roller, of which an illustration is given, was suggested to me by the maker, Francis of Colston Street, Bristol.

After a thorough trial it seems to me to present many advantages over the various rollers in use at the present time.

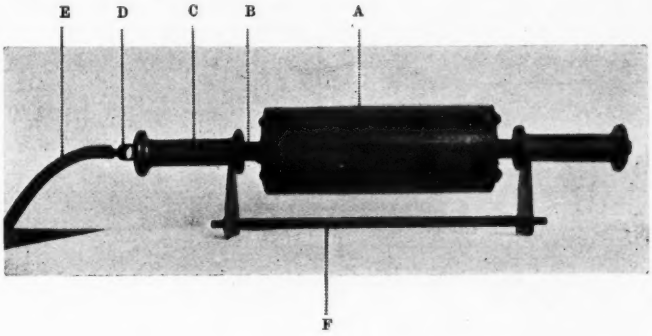

Fig. 1.

A, barrel of roller; B, axle; C, handle; D, bunsen; E, gas tube; F, stand.

As will be seen from the accompanying illustration, the barrel of the roller is of considerable diameter—some 4 inches, and it is heavy. The axle is hollow and perforated within the barrel of the roller to form the oven. Gas is led to the axle through a tube, and it passes on its way a Bunsen which is fitted to the axle. The handles are fitted to the axle. A stand is supplied on which the roller may rest. The axial position of the handles enables one to work the roller with great ease, and the gas may be turned up or down to vary the temperature. The price is 35s. for a 24-inch roller with stand.

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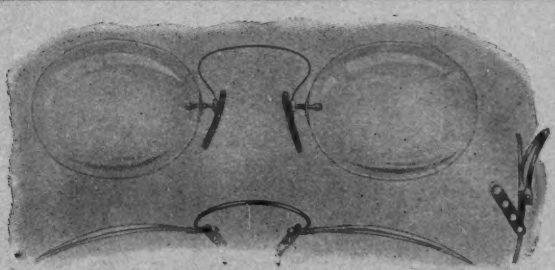

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